

**THE AMPHIPOD SUPERFAMILY PONTOPOREIOIDEA ON THE PACIFIC COAST OF NORTH AMERICA.  
I. FAMILY HAUSTORIIDAE. GENUS *Eohaustorius* J. L. BARNARD: SYSTEMATICS AND  
DISTRIBUTIONAL ECOLOGY**

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**ABSTRACT**

On the Pacific coast of North America, from the Bering Sea to Southern California, the free-burrowing gammaridean amphipod family Haustoriidae is represented by six species of *Eohaustorius* Barnard, 1957. On the Asiatic Pacific coast six species, all subtidal, have now been described. A single northern subtidal species, *E. eous*, connects the two faunas in the Bering Sea region.

This paper describes *E. barnardi*, new species, from off Pt. Conception, California, and provides re-descriptions, keys and new distributional information for *Eohaustorius eous* (Gurjanova, 1951), *E. estuarius* Bosworth, 1973, *E. sawyeri* Bosworth, 1973, *E. brevicuspis* Bosworth, 1973, *E. sencillus* Barnard, 1962 and *E. washingtonianus* (Thorsteinson, 1941). Material ascribed to the latter species from the northwestern Pacific region by Gurjanova (1962) is herewith redescribed as *E. gurjanovae*, new species. Subtidal material from South Korea is described as *E. longicarpus*, new species.

The species of *Eohaustorius* are morphologically variable throughout their ranges, especially *E. washingtonianus*, but variation is not considered of species or subspecies value. Cluster analysis reveals three main subgroupings, none very closely inter- or intra-related, viz: a North American endemic group of *E. washingtonianus* Barnard, *E. brevicuspis* Bosworth and *E. barnardi*, new species; an Asiatic Pacific group of *E. cheliferus* Bulcheva, *E. subulicolus* Hirayama and *E. robustus* Gurjanova; and a northern relatively primitive core group of *E. eous* (Gurjanova), *E. sawyeri* Bosworth, *E. gurjanovae*, new species, *E. estuarius* Bosworth, *E. longicarpus*, new species, and *E. sencillus* Barnard. The Asiatic species have relatively restricted distributions and none is intertidal. This hiatus results presumably from competition with intertidal members of amphipod family Dogielinotidae dominant in that region, and from severe physical factors in winter of low intertidal temperatures and ice scour. On the North American Pacific coast, however, all species have relatively wide geographical ranges, and four species are intertidal. There, only one species of Dogielinotidae, *Probosciniotus loquax*, provides intertidal competition, and the climate is equable year-round winter ice scour is lacking.

The genus *Eohaustorius* is sufficiently similar to North American Atlantic haustorinid genera as to preclude separate evolution from a pontoporeiid ancestor and thereby render polyphyletic the family Haustoriidae. However, the genus *Eohaustorius* is cold-temperate, and the Atlantic-endemic genera are warm-temperate, in biogeographical affinities. *Eohaustorius* is closest morphologically to the Atlantic subtidal genus *Pseudohaustorius*, thereby raising the possibility that during early Miocene times, prior to emergence of the isthmus of Panama, a common ancestor connected the two groups via a southern marine waterway.

**INTRODUCTION**

The superfamily Pontoporeioidea is a relatively small group of fossorial amphipods, whose marine members are found mainly in sedimentary substrata along holarctic shores. Members of the primitive family Pontoporeiidae tend to be arctic and sub-arctic in distribution, with a significant component confined to glacial relict freshwater lakes of North America and northwestern Eurasia (Bousfield, 1987). By contrast, members of the advanced and highly specialized family Haustoriidae are marine and estuarine and occur mainly along warm-temperate and boreal coastlines of the North Atlantic and North Pacific regions (Bousfield, 1965; 1970, 1973). On the Pacific coast of North America, family Pontoporeiidae is sparsely represented (Bousfield, in prep: *Priscillina* and *Monoporeia* in the Bering Sea, *Pontoporeia* in glacial fjords, and *Diporeia* in a few post-glacial lake basins). However, owing mainly to the work of Thorsteinson

(1941), Gurjanova (1951, 1962), Barnard (1957, 1962), Bosworth (1973) and Coyle & Mueller (1981), the family Haustoriidae is known to be moderately speciose in shallow, high energy coastal marine waters from the Bering Sea coast of Alaska to southern California. The genus is well represented in coastal waters of Korea and Japan (Ishimarus, 1994), and along the Russian coast north to the Bering Sea region, but not in Arctic waters.

Within the North Pacific region generally, the family Haustoriidae is represented only by the single genus, *Eohaustorius* Barnard, 1957. Some seven species of this genus have been recorded from the North American Pacific coast and another five from the Pacific coast of Russia and the Japan Sea (including Korea). The genus is distinct from the North Atlantic complex (with the European species *Haustorius arenarius* (Slabber) as type) in having peraeopods 3 and 4 unlike in size and form, and telson lobes widely separated on the dorsum of urosome 6, among other differences.

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This study treats the systematics and distributional ecology of species of the genus *Eohaustorius* in North Pacific coastal marine region, and emphasizes the North American Pacific fauna.

Species of *Eohaustorius* have proven useful as indicators of sediment quality (see Bousfield, 1991; Mcleay et al. (1990); Yee et al. 1992).

**Acknowledgements.** The present North American haustoriid material was accumulated mainly as a result of National Museum, now Canadian Museum of Nature (CMN), field expeditions, conducted by one of us (ELB) and colleagues, during the period 1955-1980. Complete lists of stations, pertinent data and acknowledgement of field assistance are provided elsewhere (Bousfield, 1958, 1963, 1968; Bousfield & McAllister, 1962; and Bousfield & Jarrett, 1981). Additional material was provided by Drs Peter Slattery, Moss Landing, California; Charles O' Clair, Auke Bay, Alaska; Kathleen Conlan CMN, Ottawa, and McLeay Associates, West Vancouver. The authors are most grateful for use of the laboratory facilities of Dr D. V. Ellis, University of Victoria, and for the use of collections and facilities of the CMN in Ottawa.

The authors are indebted to Dr Weldon S. Bosworth for his pioneering work on much of this material in 1973-4, and for his unpublished commentary and distributional information. Susan Laurie-Bourque very capably assisted in preparation of the line drawings. Marjorie A. Bousfield provided translations of pertinent Russian literature. The illustrative work was supported under a research divisional grant of the Royal Ontario Museum, Toronto.

## SYSTEMATICS

### *Haustoriidae* Stebbing

*Haustoriidae* Stebbing, 1906: 118.—Gurjanova, 1951: 328; 1962: 395.—Bousfield, 1965: 165 (part); 1973: 99 (part); 1982: 259.—Barnard and Drummond, 1982: 136.—Hirayama, 1985: 395.—Barnard & Karaman, 1991: 357.

**Taxonomic commentary.** Barnard and Karaman (1991) have provided a simplified key to genera of *Haustoriidae* (*sensu strictu*).

With respect to superfamily classification, Barnard & Karaman (*loc. cit.*) have continued recognition of family *Haustoriidae* as the type of superfamily *Haustorioidea*, proposed initially by Barnard & Drummond (1982). As shown by Bousfield (1982b, 1990) and Bousfield & Shih (1994), the Barnardian concept (of *Haustorioidea*) includes most members of family *Urothoidae* and other superficially and convergently similar families. The latter groups are phylogenetically more correctly placed within superfamily *Phoxocephaloidea* (e.g., Bousfield 1982, 1990; and Schram, 1986). In all major character states, family *Haustoriidae* is most clearly related to members of family *Pontoporeiidae*,

and thus phylogenetically assignable to the superfamily which the latter typifies, the *Pontoporeioidea*. As shown above (Bousfield, *loc. cit.*), these major *pontoporeioidean* character states of *Haustoriidae*, especially of its most primitive genus *Protohaustorius*, include its short broad, weakly rostrate head, "pseudorostrate" paired peduncles of antenna 1, weakly (or non-) dactylate peraeopods and maxilliped, lack of coxal gill on peraeopod 7, unique form of the pleopods (lacking clothespin spines), strongly deflexed urosome, and the holarctic (non-antipodean) distribution of nearly all member species. The character states of the *Pontoporeioidea*, especially the phylogenetically significant antennal calceoli, are basically *gammarioidean* and not *phoxocephaloidean* or *crangonyctoidean* in form.

### *Eohaustorius* J. L. Barnard

*Eohaustorius* J. L. Barnard, 1957: 81.—Gurjanova, 1962: 400.—Bousfield, 1970: 150.—Bosworth, 1973: 160.—Barnard, 1975: 348 (key).—Hirayama, 1985: 43.—Barnard & Karaman, 1991: 361.—Ishimaru, 1994: 64.

**Type species.** *Haustorius washingtonianus* Thorsteinson, 1941, original designation.

**Component species.** *E. tandeensis* Dang, 1968; *E. subulicolus* Hirayama, 1985; *E. cheliferus* (Bulycheva, 1952); *E. eous* (Gurjanova, 1951); *E. robustus* (Gurjanova, 1953); *E. sawyeri* Bosworth, 1973; *E. brevicuspis* Bosworth, 1973; *E. estuarius* Bosworth, 1973; *E. longicarpus*, new species; *E. gurjanovae*, new species; *E. sencillus* Barnard, 1962; *E. barnardi*, new species.

**Diagnosis.** Body short, broad. Head broad; rostrum short, acute. Pigmented eyes essentially lacking. Antenna 1, flagellum 5-segmented; accessory flagellum 2-segmented, attached subapically to peduncular segment 3, bearing aesthetascs. Antenna 2, peduncle 4 broadly lobate and strongly setose behind; peduncle 5 broad, not lobate behind; flagellum 4-5 segmented.

Upper lip rounded. Lower lip, inner lobes with short proximal processes. Mandible, molar strong triturate; incisor acute; palp segment 3 with few (5-15) inner marginal comb spines. Maxilla 1 lacking accessory basal baler lobe; inner plate with single apical seta; outer plate with 8-9 apical spines. Maxilla 2, outer plate little larger than inner, not lunate in form; inner plate with weak facial setae. Maxilliped, inner plate with 2 apical spines; outer plate very large, exceeding palp segment 2; palp segment 3 clavate, not geniculate.

Coxal plates 1 & 2 small, 3 & 4 squarish below. Gnathopod 1, segment 3 very short; segment 5 relatively short, deep; segment 6 medially deepest. Gnathopod 2, segment 3 very short; segment 5 with postero-distal cluster of specialized spines; segment 6 short, medially swollen, arcuate, produced beneath minute dactyl to form a microchela.

KEY TO NORTH PACIFIC SPECIES OF *EOHAUSTORIUS*

1. Pleon plate 3 strongly produced behind into a recurved hooklike process; peraeopod 4, hind lobe of segment 5 elongate, slender, length 4-5 X width (depth); uropod 3, inner ramus with single small inner marginal seta; Asiatic coast. . . . . *E. subulicolus* (p. 42)  
 —Pleon plate 3, hind process nearly straight, if hooked, not recurved; peraeopod 4, segment 5, hind lobe shorter, deeper, length less than 2 X depth; uropod 3, inner margin with 2-6 setae . . . . . 2.
2. Peraeopod 6, segment 4 tall, length 2X width, with 5-6 groups of facial spines (in addition to marginal spines); basis slender, distinctly narrower than length (depth), subovate; uropod 1, hind margin of inner ramus with 2 single setae; gnathopod 1, dactyl, body large, length > nail (unguis) . . . . . 3.  
 —Peraeopod 6, segment 4 subtriangular, widest distally, length < 2X width; basis as broader or broader than length; gnathopod 1, dactyl, nail longer than body. . . . . 4.
3. Antennae 1 & 2, flagella 5-segmented; peraeopod 4, hind lobe elongate, ~2 X depth; abdominal side plate 3, apex abruptly upturned, minutely split-tipped . . . . . *E. longicarpus* (p. 56)  
 —Antenna 1 & 2, flagella 3-segmented; peraeopod 4, segment 5, hind lobe short, length not greater than depth; abdominal side plate 3, hind process straight or apex slightly upturned . . . . . *E. sencillus* (p. 44)
4. Peraeopod 4, segment 5, posterior lobe, distal margin with spine cluster; peraeopod 6, segment 4 with lower facial row of 2-3 spine groups; peraeopod 6, segment 5 with posterior marginal spine group . . . 7.  
 —Peraeopod 4, segment 5, distal lobe base, smooth; peraeopod 6, segment 4 with at least one other spine cluster above lower row; peraeopod 6, segment 5 lacking posterior marginal spines . . . . . 5.
5. Peraeopod 7, basis, hind margin proximally with strong cusp or tooth; pleon plate 3 produced, posteriorly as weak tooth . . . . . *E. washingtonianus* (p. 50)  
 —Peraeopod 7, basis hind marginal tooth weak or rounded; pleon plate 3, process strong . . . . . 6.
6. Peraeopod 7, basis wider than deep, hind cusp rounded; maxilliped palp, segment 3 strongly broadened distally, width = 3/4 length . . . . . *E. brevicuspis* (p. 50)  
 —Peraeopod 7, basis not wider than deep, hind cusp acute; maxilliped palp, segment 3 normal, length ~2X width . . . . . *E. barnardi* (p. 54)
7. Peraeopod 4, segment 5, hind lobe strongly produced, width of segment 2 X depth (length); peraeopod 7, segment 6 with 2 posterior marginal groups of spines; gnathopod 2, basis, hind margin with distal setae only . . . . . *E. cheliferus* (p. 55)  
 —Peraeopod 4, segment 5, hind lobe normal, width about equal to length; peraeopod 7, segment 6 with 3-4 posterior marginal spine groups; gnathopod 2, basis, hind margin setose throughout . . . . . 8.
8. Peraeopod 5, segment 4 widest distally, 2X length; pleon plate 3, postero-dorsal process large, strongly overhanging urosome; uropod 3, inner ramus with 2-3 marginal setae . . . . . *E. sawyeri* (p. 44)  
 —Peraeopod 5, segment 4 less broad, ~ 1.5X length; pleon overhang normal, little or not exceeding side plate process; uropod 3, inner ramus with 5 marginal setae . . . . . 9.
9. Peraeopod 7, segment 6 with 2 groups of posterior marginal spine groups; coxae 3 & 4 antero-distal margins rounded . . . . . *E. estuarius* (p. 40)  
 —Peraeopod 7, segment 6 with 3-4 posterior marginal spine groups; coxae 3 & 4 squarish . . . . . 10.
10. Peraeopod 5, segment 6 with 1 group of anterior marginal spines; pleon plate 3, hind process, apex slightly upturned; peraeopod 4, segments 5 & 6 lacking anterior marginal spines; peraeopod 7, basis very broad, exceeding length . . . . . *E. robustus* (p. 48)  
 —Peraeopod 5, segment 6 with 2 groups anterior marginal spines; pleon plate 3 hind process straight; peraeopod 4, segment 5 & 6 with anterior marginal spines; peraeopod 7, basis not wider than deep . . . . 11.

11. Peraeopod 7, segment 6 with 4 posterior marginal spines; basis lacking posterior cusp; mandibular palp segment 3 with 14-15 posterior marginal comb spines . . . . . *E. eous* (p. 38)  
 —Peraeopod 7, segment 6 with 3 posterior marginal spines; basis with rounded posterior proximal cusp; mandibular palp segment 3 with 8-9 posterior marginal comb spines . . . . . *E. gurjanovae* (p. 47)

Peraeopod 3, segment 4 short, triangular; 5 weakly lobate behind; 6 small, margins spinose, not setose. Peraeopod 4 smaller and unlike peraeopod 3 in form; segment 3 very short, 4 little broadened, 5 strongly produced and spinose behind; 6 slender, distally spinose and setose.

Peraeopod 5, basis broad, hind margin setose, with proximal cusp; segments 4-6 not broader than long, outer face with spine clusters. Peraeopod 6 longest; basis medium broad, hind margin setose, with proximal cusp; segment 4 often longer than broad; segment 5 broader than long, with prominent antero-distal process and distal marginal notch; segment 6, some distal spines split-tipped. Peraeopod 7, basis very broad hind margin nearly bare, proximal cusp low or lacking; segment 4 broad, triangular; segment 5 broad.

Pleon segment 3 strongly deflexed posteriorly, postero-distal lobe strong, overhanging urosome. Pleon plate 3, hind corner acutely produced. Pleopods powerful; peduncle short, broad; outer ramus 10-16 segmented, inner shorter, with proximal baso-medial lobe.

Urosome short, lacking antero-distal lappet. Uropod 1, rami cylindrical, inner ramus with posterior marginal setae only. Urosome 2 short, not occluded dorsally. Uropod 2, rami heavily setose, subequal. Uropod 3, rami short, <2X peduncle, terminal segment variable. Telson lobes widely separated at base; each with dorso-lateral marginal setae, and single apical penicillate seta.

Coxal gills saclike, on peraeopods 2-6. Brood plates relatively narrow, elongate.

**Distribution.** Member species are endemic to the North Pacific coastal shelf regions of eastern Asia, and North America, from the Bering Sea to Vietnam in the west, and in the east, south to Baja California.

**Taxonomic commentary.** *Eohaustorius* is distinct from North American Atlantic genera in the unlike form of peraeopods 3 & 4 and the widely separated telson lobes. However, in the short antennal flagella, form of the lower lip, maxilla 1 & 2, maxilliped, processiferous pleon plate 3, and setose telson, it more closely resembles the warm-temperate North Atlantic genus *Pseudohaustorius* (Fig. 2, p. 41) than the type genus *Haustorius* (Fig. 2.2). Such basic similarities suggest a former ancestral link with the diverse Atlantic haustoriid complex via the submerged Panama isthmus (Bousfield, 1970) (see also pp. 61-62).

*Eohaustorius eous* (Gurjanova)  
 (Figs. 1, 2)

*Haustorius eous* Gurjanova, 1951: 331.  
*Eohaustorius eous eous* Gurjanova, 1962: 406.  
*Eohaustorius eous* Barnard & Karaman, 1991: 463.—Ishimaru, 1994: 64.

**LEGEND FOR FIGURES**

A1	-	antenna 1	MX 1	-	maxilla 1
A2	-	antenna 2	MX2	-	maxilla 2
BR.	-	coxal gill	MXPD	-	maxilliped
BR SET	-	brood plate seta	O. P.	-	outer plate
COXAE	-	coxal plates	PLP	-	palp
DACT	-	dactyl	P3-P7	-	peraeop'ds 3-7
EP 1-3	-	pleon plates 1-3	RT	-	right
GN1	-	gnathopod 1	SP	-	spine
GN2	-	gnathopod 2	T	-	telson
I. P.	-	inner plate	U1-U3	-	uropods 1-3
I. R.	-	inner ramus	UROS	-	urosome
LFT	-	left	X	-	magnified
LL	-	lower lip	o	-	male
MD	-	mandible	o	-	female

**Material examined.**

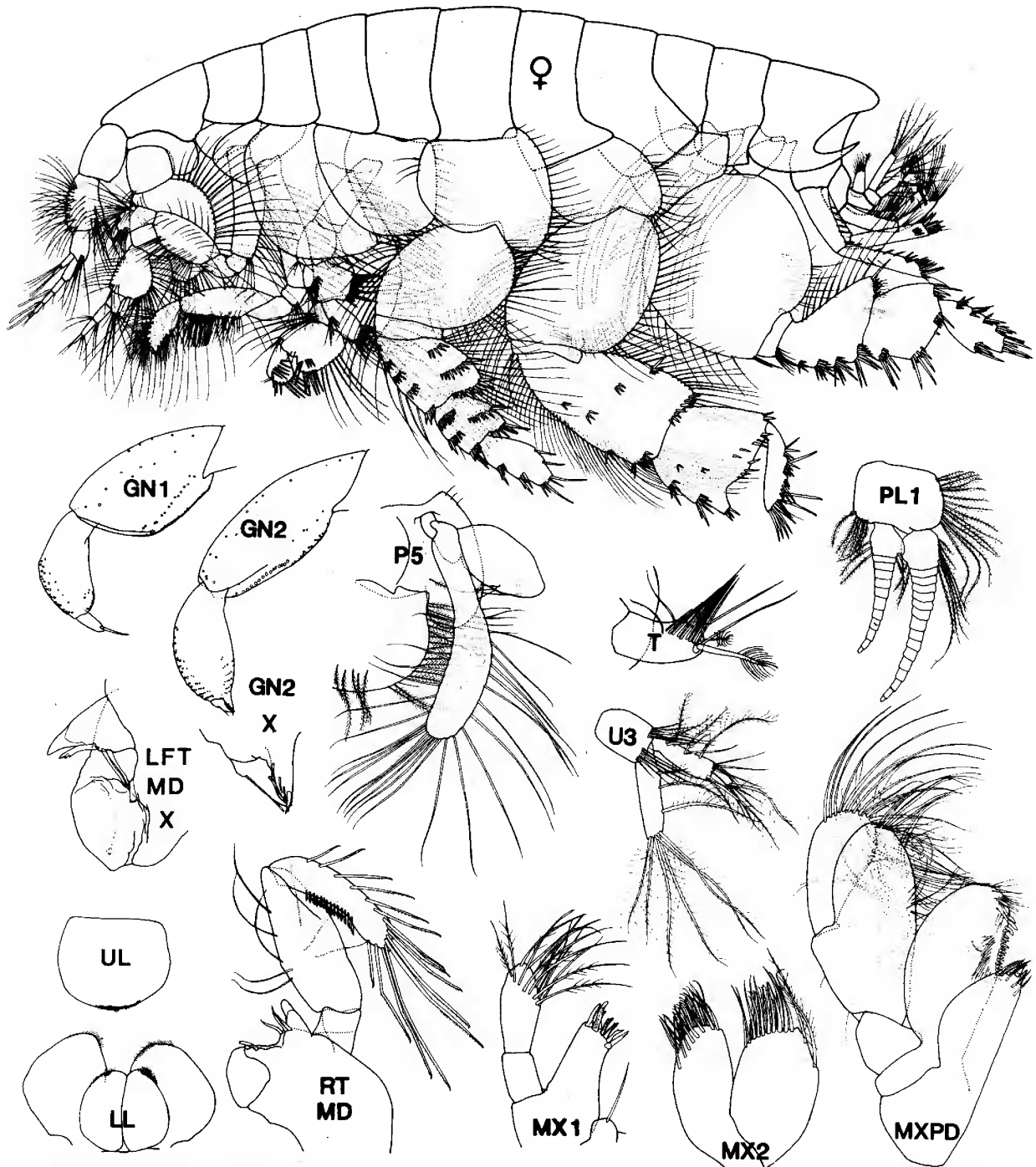
ALASKA. Bering Sea: Northeast end of St. Lawrence I., Lot #1, 20 m sand, P. Slattery coll., July 10, 1980 - 2 males, 4 females, 1 im, CMN Cat. no. NMCC1991-1209; *Ibid.*, Lot#5 - 2 males, 13 female, 5 im.  
 St. Mathew I., Walrus Cove, sand, 8 m, P. Slattery coll., 1983 - 1 im; *Ibid.*, 11 m scoop, sand - 3 males, 11 females, 2 im; *Ibid.*, 13 m, sand - 2 males, 21 females, 14 im. CMN Cat. no. NMCC1991-1206.  
 St. Paul I., English Bay, 3 m scoop, P. Slattery coll., 1983, - 5 males, 37 females, 8 im; *Ibid.*, 10 m sand - 3 males, 9 females, 2 im; *Ibid.*, reef, 20 m - 1 female ov (5.5 mm) slide mount, 3 females (5.5 mm, 5.5 mm, 4.5 mm)+ 1 male, 4 females, 15 im, NCMNB Cat. no. NMCC1991-1204; *Ibid.*, 25 m sand - 3 males, 36 females, 15 im, CMN Cat. no. NMCC1991-1203.  
 Alaska mainland: 30 miles west Cape Rodney, 24 m. dive, P. Slattery coll., 1981 - 6 females, 3 im, CMN Cat. no. NMCC-1991-1211.

**Diagnosis.** Female (6.0 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, segment 2 strongly setose anteriorly; accessory flagellum inserted nearly apically. Antenna 2, peduncular segment 4, postero-distal lobe medium; posterior margin lined with numerous (>40) plumose setae; segment 5 medium broad, widest distally; flagellar segment 1 with postero-distal setal cluster.

Mandible, palp segment 3 with 14-15 posterior marginal comb spines. Maxilla 2, inner plate with distinct facial row of 6-7 plumose setae. Maxilliped, outer plate medium; palp segment 2, inner lobe large, broad, reaching almost to tip of narrowly clavate segment 3.

Coxae 1 & 2. Gnathopod 1, segment 5 relatively short, deep; segment 6 medium, arcuate. Gnathopod 2, hind margin long-setose; segment 5 slender, shallow, distal spines slender.

Peraeopod 3, coxa squarish; segment 4 short, distally broad; segment 5 strongly setose proximally; segment 6



**FIG. 1. *Eohaustorius eous*. (Gurjanova). Female ov. (5.0 mm). Bering Sea, Alaska. Slattery coll.**

ovate, margins spinose. Peraeopod 4, segment 4 with 23 posterior marginal setae; segment 4 hind lobe short, distally broad, truncate, anterior margin with 1 stout spine group; segment 6 slender, with 21 anterior marginal spine group.

Peraeopod 5, basis broadly ovate, hind margin completely lined with setae; segment 4 short, uniformly broad; facial spine clusters strong; segment 5 medium, not wider than long, facial spine clusters strong; segment 6 broadest medially, anterior margin with 2 spine clusters, posterior margin with 2 single spines. Peraeopod 6, basis medium, hind margin setose throughout; segment 4 elongate, with 3-4 facial spine clusters; segment 5 broadest distally, with 2

weak facial spine groups, 4-5 inner distal and 5-6 outer distal marginal spines; antero-distal emargination medium deep; segment 6 relatively long and slender, with 4-5 clusters of mixed long and short spines. Peraeopod 7, basis broad, hind margin distally narrowing and lined with medium setae; segment 4 slightly wider than long, anterior margin with 3 spine clusters, posterior margin lined with long setae; segment 5 squarish, anterior margin with 1 cluster of long spines; segment 6 little broadened, anterior margin with 1, and posterior margin with 4, clusters of medium spines.

Pleopods, basis stout, broad, outer margin strongly plumose-setose; outer ramus 15-segmented, inner 12-seg-

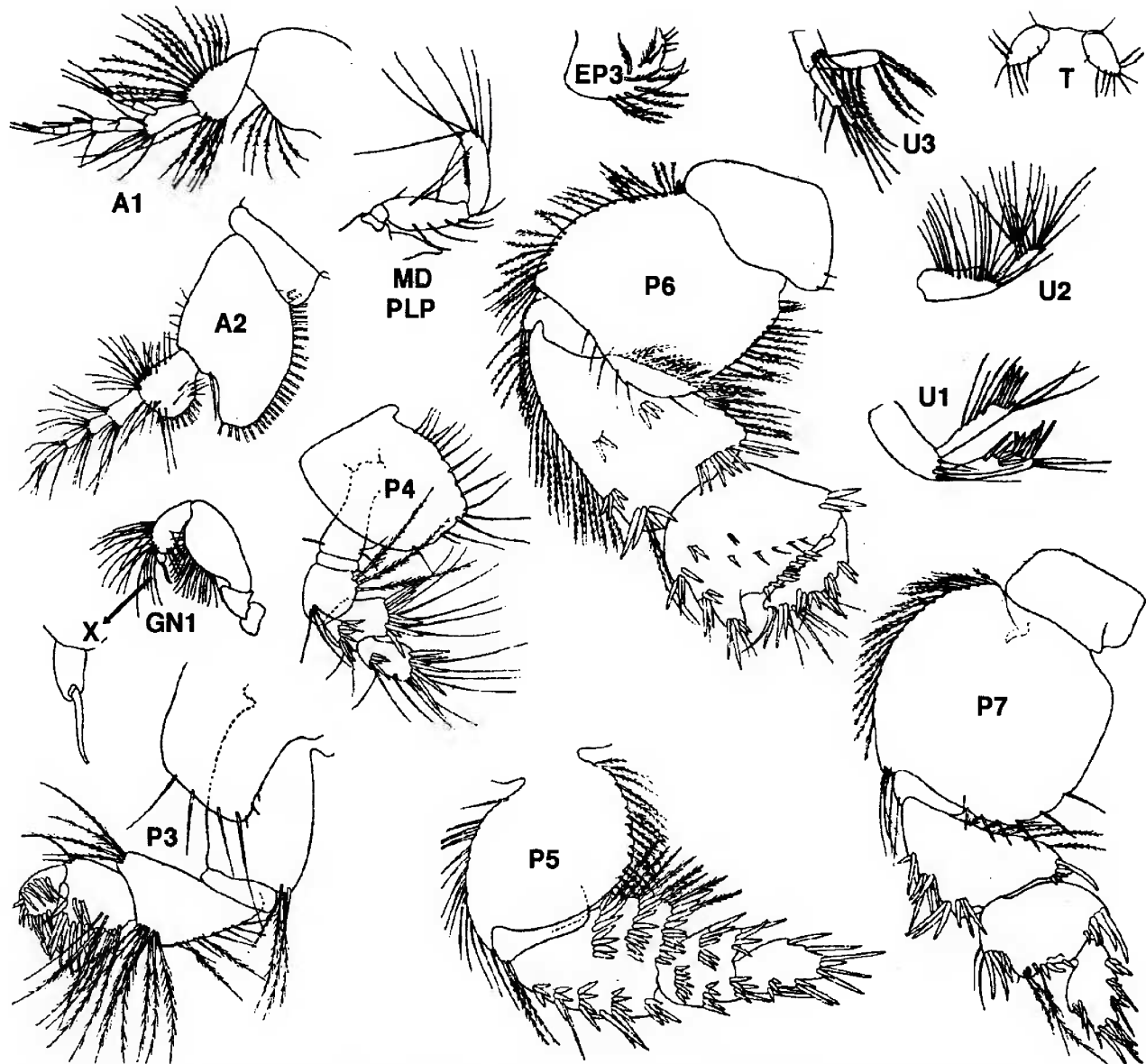


FIG. 2 *Eohaustorius eous* (Gurjanova) Female ov. (6.0 mm). East coast Kamchatka peninsula. (after Gurjanova, 1962)

mented. Pleon plate 3, hind corner strongly produced, nearly straight, acute. Uropod 1, peduncle, outer margin with 4-5 slender spines; inner ramus, posterior margin with short spines. Uropod 3, outer ramus, terminal segment short (<1/2 proximal segment); inner ramus, inner margin with 3 plumose setae.

Telson lobes short, slender, with 12 dorso-distal setae.

**Distribution.** Eastern Kamchatka & Bering Sea, 20-40 m; western Bering Sea, subtidally to 25 m. Not taken in southeastern Alaska despite apparently suitable habitat (e.g., Glacier Bay) where *E. washingtonianus* was dominant.

**Taxonomic commentary.** *E. eous* is a relatively primitive species, showing several plesiomorphic character states in common with the N. America estuarine species *E. estuarius*. It is not closely related to *E. robustus*, differing in the character states noted in the key and on p. 37. The material

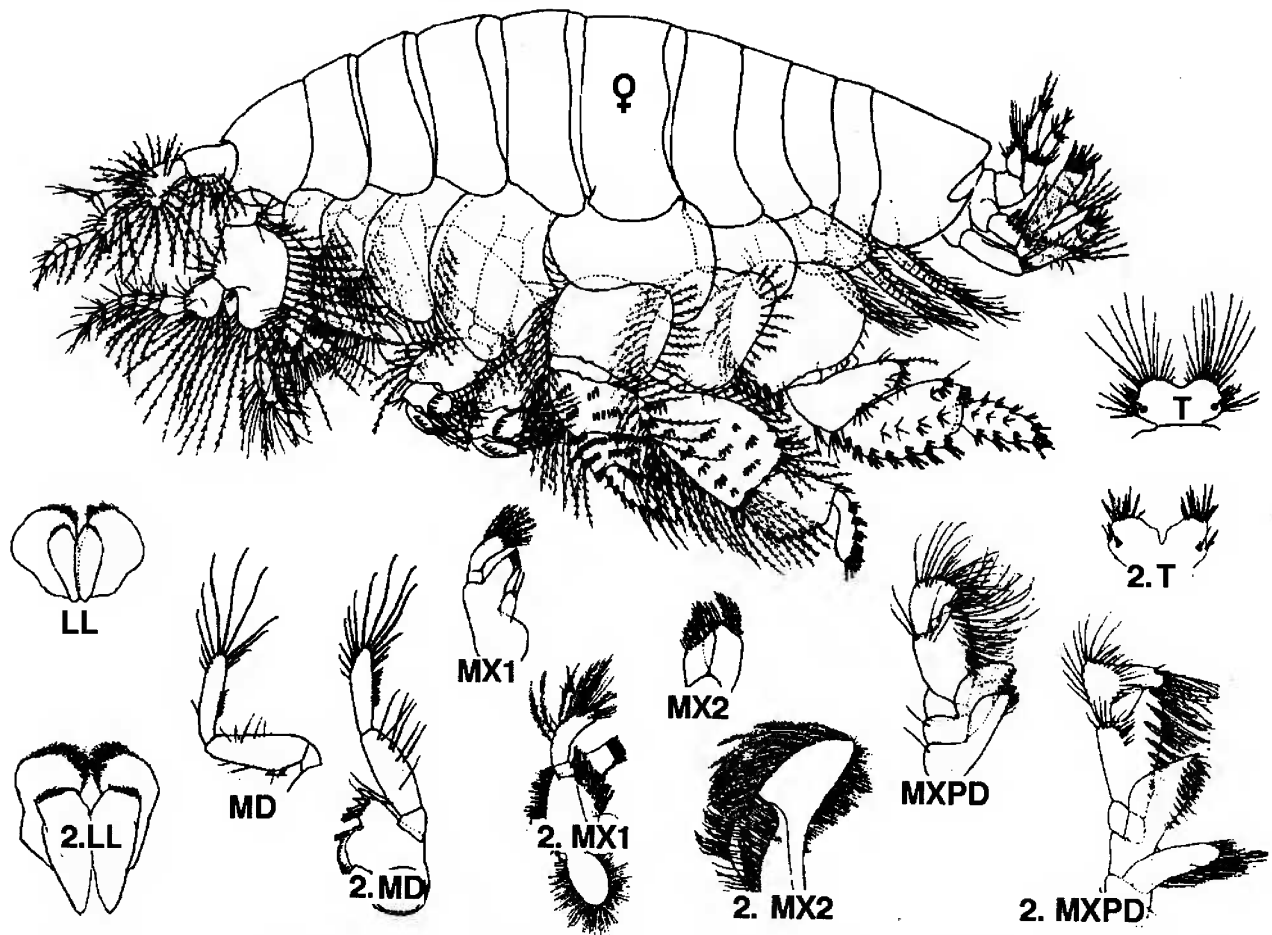
from the northern Sea of Okhotsk, illustrated in Gurjanova (loc. cit., fig. 136B2) is here considered a variant on the main theme from the Kamchatka peninsula and Bering Sea regions.

*Eohaustorius estuarius* Bosworth  
(Figs. 4)

*Eohaustorius estuarius* Bosworth, 1973: 253, fig. 2 im.—Staude, 1987: 372 (key), 383, fig. 18.11.—Barnard & Karaman, 1991: 363.

**Material examined.** 10 lots containing 158 specimens: BRITISH COLUMBIA.

Queen Charlotte Islands, ELB Stns., July-Aug., 1957 (~10 specimens at 3 stations, verified by W. Bosworth, 1973): H8a (Delkatla Slough) - 3 females; H10 (New Masset) - 1 female; W1 (north end Lepas Bay) - 8 males 12 females, 6 im. Vancouver I., north end, ELB Stns., 1959: O12, Ahous Bay,



**FIG. 3.** *Pseudohaustorius caroliniensis* Bousfield. Female (7.6 mm), lateral view; mouthparts, telson  
**2.** *Haustorius canadensis* Bousfield. Female (12.0 mm), mouthparts, telson. (after Bousfield, 1973).

Vargas I. - 3 males, 1 fem, 1 im; Stn. O13, Yarksis, Vargas I. - 4 males, 5 females, 1 im.  
 Central Vancouver I., ELB Stns., 1955: P1, Clayoquot I. - 1 female, 1 im; P6a, southeast end Wickaninnish Bay - 11 males, 26 females. ELB Stns., July, 1970: P701, south end Long Beach, in surf-exposed sand at freshwater beach seep, LW level - 1 female ov. (5.0 mm), (slide mount) (**fig'd specimen**), + 17 males, 33 females, CMN Cat. no. NMCC1991-1229; P708, Pachena Bay, mouth of estuary - numerous specimens.

**WASHINGTON, OREGON.**

ELB Stn. W34, Crescent Beach, east end, near creek mouth - 1 female (4.8 mm), slide mount, +12 other females, 5 males, CMN Cat. no. NMCC-1992-1255; Stn. W41, Sooes estuary, near mouth, in steep sand banks - 1 im.

**Diagnosis.** Female (5.0 mm): Head, rostrum medium; eyes small, weakly pigmented. Antenna 1, peduncle 2, anterior margin setose nearly to base. Antenna 2, peduncular segment 4, postero-distal lobe large, posterior margin with 25+ plumose setae; segment 5 distally broadest; flagellar segment 1 with distal plumose seta.

Mandible, palp segment 3, inner (posterior) margin with

10-12 marginal comb spines, outer margin with 5-6 mediums etae. Maxilla 2, inner plate with strong facial row of setae. Maxilliped, inner plate tall, slender; outer plate broad, distally truncate; palp segment 2, inner lobe long narrow, reaching tip of broadly expanded palp segment 3.

Gnathopod 1, basis, anterior margin weakly setose throughout; carpus short, deep; dactyl, nail long. Gnathopod 2, carpus relatively short and deep, with sub-apical postero-distal cluster of slender spines.

Peraeopod 3, coxae expanded anteriorly, basis with antero-distal cluster of setae. Peraeopod 4, segment 4 with 2 posterior marginal plumose setae; segment 5, hind lobe medium, proximal margin with a few setae, anterior margin with strong oblique spine row, hind margin truncate, spinose; segment 6 medium, little broadened distally, with single oblique anterior marginal spine group.

Peraeopod 5, coxal hind margin strongly setose; basis medium, hind margin proximally setose; segment 4 relatively short, broad, facial spine groups strong; segment 5 shorter than broad, facial spines strong; segment 6 broadest medially, with 2 anterior marginal spine groups, hind margin with single spine cluster. Peraeopod 6, basis medium, hind margin distally bare; segment 4 relatively short, broadest distally, with 4 weak facial groups of spines; segment 5

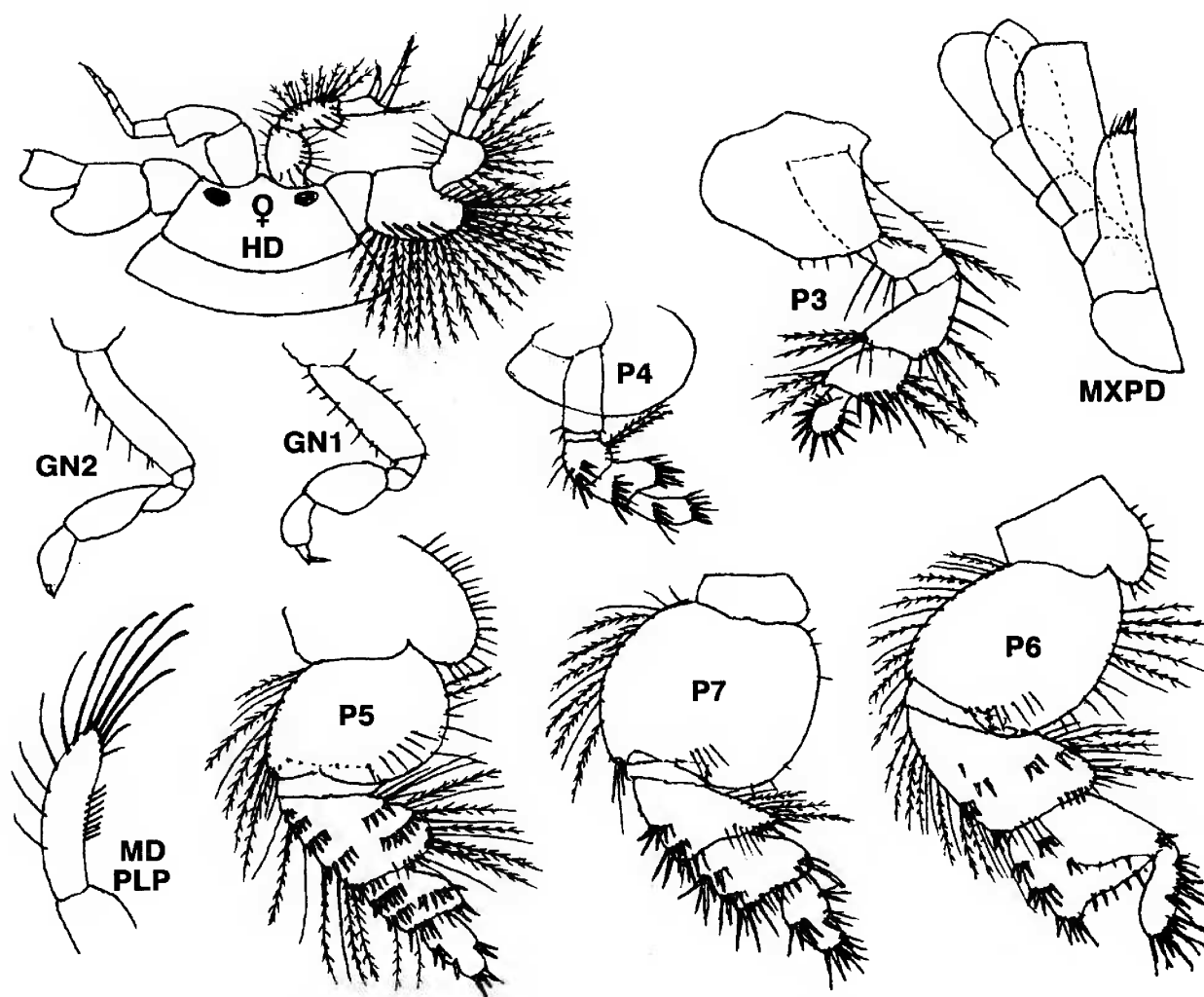


FIG. 4. *Eohaustorius estuarius* Bosworth, Female ov (5.0 mm) Long Beach, V. I., B. C. (partly after Bosworth, 1973)

broader than deep, with 2 small facial clusters of spines, 3-4 spines along inner distal margin, and 9-10 spines along outer distal margin; segment 6 with 6-7 posterior marginal clusters of short and long spines. Pereopod 7, basis broadly expanded, lacking proximal basal cusp, hind margin nearly bare; segment 4 short, very broad distally, anterior margin with 2 spine clusters, posterior margin lined with plumose setae throughout; segment 5 short, broader than deep, with 2 anterior marginal spine clusters; segment 6 broad, anterior margin strongly convex with single cluster of strong spines, posterior margin with 2 spine clusters.

Pleopods normal for the genus. Pleon plate 3, hind corner strongly produced, straight, acute. Uropod 3 rami relatively short, <2X peduncle; outer ramus medium; inner ramus with few inner marginal seta.

Telson lobes medium broad, regularly setose.

**Distribution.** Common in freshwater intertidal seeps and rills over open and/or protected sand beaches, from Central California north through Oregon, Washington, and British Columbia to Dixon Entrance; not yet taken in south-eastern Alaska.

**Taxonomic commentary.** As noted elsewhere (p. 59), this species shows mainly plesiomorphic character states. It is a member of the *E. eous* subgroup and similar to *E. gurjanovae* of the Asiatic North Pacific region..

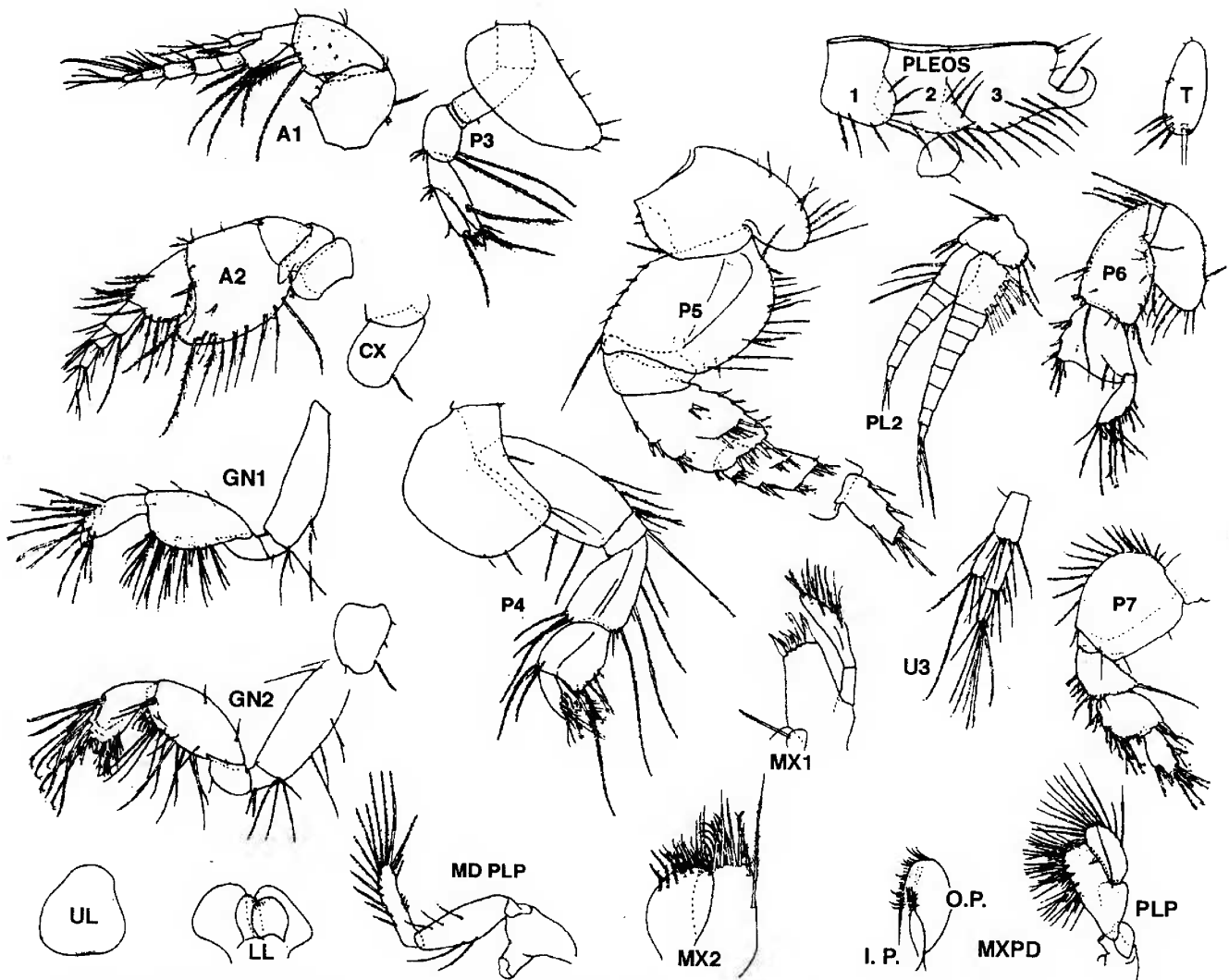
*Eohaustorius subulicolus* Hirayama  
(Fig. 5)

*Eohaustorius subulicola* Hirayama, 1985: 43, figs. 155-157.  
*Eohaustorius subulicolus* Barnard & Karaman, 1991: 463.—  
Ishimaru, 1994: 64.

**Diagnosis.** Male (2.25 mm): Head, rostrum short, decurved. Pigmented eyes lacking. Antenna 1, accessory flagellum medially inserted on peduncular segment 3. Antenna 2, peduncular segment 4, antero-distal lobe shallow; hind margin with few (~17) plumose setae; segment 5 of medium width; flagellar segment 1 with single large postero-distal seta.

Mandibular palp, segment 3 with few (4-5) comb spines. Maxilla 1, outer plate with 8 apical spines. Maxilla 2, inner plate with 6-7 submarginal facial row of setae. Maxilliped,





**FIG. 5.** *Eohaustorius subulicolus* Hirayama. Male (2.25 mm). Tomioka Bay. (after Hirayama, 1985).

palp segment 3 narrowly clavate; outer plate narrow.

Coxa 1 vestigial; coxa 2 small rounded below, hind margin with single seta. Gnathopod 1, segment 5 short and deep; segment 5 slender. Gnathopod 2, basis with ~5 hind marginal setae; segment 5 with 5 distally spoon-shaped spines.

Peraeopod 3, basis, hind margin with distal setae only; segment 5, hind margin lacking proximal setae; segment 6 narrow. Peraeopod 4, coxa slender smoothly convex in front; basis hind margin bare; segment 4 with 4 posterior marginal setae; segment 5 (carpus), posterior lobe slender acute, lacking spines; segment 6 slender, with apical spine(s) only.

Peraeopod 5, basis, posterior margin setose throughout; segment 4 narrow, longer than broad, facial spines medium; segment 5 slender; segment 6 slender, with single anterior marginal spine. Peraeopod 6, basis, hind margin setose throughout; segment 4 little broadened, facial spines lacking; segment 5 broadest distally, lacking facial spines, distal margin with a few spines near hinge; segment 6, postero-distally with slender split-tipped spines and long setae. Peraeopod 7, basis lacking proximal cusp, hind margin straight,

nearly bare; segment 4 slender, hind margin nearly bare; segment 5 as long as broad, anterior margin with 3-4 slender spine groups; segment 6 slender with single anterior marginal spine cluster and elongate pectinate apical spines.

Pleopods, peduncle small; rami slender, outer ramus 9-10-segmented. Pleon plate 3, hind corner strongly produced, hooklike, extending well beyond postero-dorsal process. Uropod 1, rami with apical spines and setae. Uropod 3, rami slender; inner ramus lacking inner marginal setae; outer ramus, terminal segment strong (> 2/3 inner segment).

Telson lobes slender, marginal setae few.

**Distribution.** Tomioka Bay, Japan; subtidal.

**Taxonomic commentary.** *Eohaustorius subulicolus* is distinctive on the basis of reduction of some character states, and special development of others. Hirayama (1985) described the species from the type male and four additional specimens. He noted its general resemblance to *E. cheliferus*, but *E. subulicolus* may qualify for separate subgeneric status.

*Eohaustorius sawyeri*, Bosworth  
(Fig. 6)

*Eohaustorius sawyeri* Bosworth, 1973: 257, fig. 1a-e.—Austin, 1985: 607.—Staude, 1987: 383, 372 (key).—Barnard & Karaman, 1991: 363.

**Material examined.** Six lots containing 37 specimens (both sexes and subadults), from 4 localities in British Columbia, and two in California:

BRITISH COLUMBIA.

Vancouver I., southern end: Off Long Beach, V. I., 22 m, P. Slattery Stn., 1982 - 3 males, CMN Cat. no. NMCC1991-1219. ELB Stn. P21a, Trevor Channel, off Bordelais I., 44 m, fine sand, Aug. 9, 1975 - 1 female (3.2 mm) (slide mount) (**figured specimen**), CMN Cat. no. NMCC1991-1227; *Ibid.*, Stn. B9c, off Second beach, 20-25 m, medium sand, June 28, 1976 - 1 female; ELB Stn. H41, Jordan R., black silty sand, LW, July 27, 1964 - female ov (5.2 mm).

CALIFORNIA

Off Marine Laboratory, Moss Landing, 2 m sand, P. Slattery coll., June 1, 1982 - 2 males, 7 females, CMN Cat. no. NMCC1991-1240; *Ibid.*, 12 m, July 1, 1982 - 5 males, 8 females, CMN Cat. no. NMC1991-1239.

**Diagnosis.** Female im. (3.2 mm.): Head, rostrum. Eyes whitish, not pigmented. Antenna 1, peduncle 2, anterior margin weakly setose, singly inserted. Antenna 2, peduncle 4, postero-distal lobe medium, posterior margin with 30+ plumose setae, antero-distal lobe strong, extending >2/3 length of segment 5; segment 5 relatively shallow; basal flagellar segment with 3-4 distal plumose seta.

Mandible, palp segment 3 with 8-11 posterior marginal comb spines. Maxilla 1, palp stout, proximal segment short (<1/2 segment 2). Maxilla 2, inner plate, facial setae submarginal. Maxilliped, outer plate medium; palp segment 2, inner lobe narrow, shorter than medium-large segment 3.

Gnathopod 1, coxa subquadrate; basis broadened medially, anterior margin smooth distally; segment 5 elongate, medium deep; segment 6, thick (deep). Gnathopod 2, basis, anterior margin smooth; segment 5 slender, lower margin straight.

Peraeopod 3, coxa 3 subquadrate; segment 4 short, very broad distally; segment 5 deep, with antero-proximal invagination, hind margin proximally setose; segment 6 large, lozenge-shaped, margins slender-spinose. Peraeopod 4, segment 4 with 4 postero-marginal setae; anterior margin with distal spine group; segment 5, anterior margin with fan-wise spine row, hind lobe short, postero-proximal margin with 2 spine clusters; segment 6 stout, broadening distally, with 2 anterior and 2 posterior marginal spine clusters.

Peraeopod 5, basis broadly ovate, hind margin nearly bare distally; segment 4 short, strongly broadest distally, facial spines strong; segment 5 expanding distally, longer than broad, facial spines strong; segment 6 broad, apex truncate, anterior margin with 1, posterior margin with 3

spine clusters. Peraeopod 6, basis medium broad, hind margin lightly setose proximally; segment 4 long, broadest distally, with several strong facial spine clusters; segment 5 broadening distally, with 2 strong facial spine clusters antero-distal margin with 12-15 spines, excavation shallow; segment 6 slender, with 4-5 posterior marginal spine clusters. Peraeopod 7, posterior margin of coxa broadly acute; basis broad, convex hind margin distally with a few short setae, lacking proximal cusp; segment 4 short, broadest distally, hind margin setose; segment 5 broader than deep, anterior margin with single spine group, antero-distal free margin broad, lined with spines, postero-distal angle with long heavy spine; segment 6 broad, anterior margin with 1, posterior margin with 3-4 stout spine groups.

Pleopods, peduncle short broad, outer margin strongly plumose-setose; outer ramus 16-segmented, inner ramus 13-segmented. Pleon plate 3, hind corner moderately produced, acute, strongly overhung by, and much shorter than, postero-dorsal process of pleosome 3. Uropod 1, peduncle, outer margin with 3-4 slender spines, distal spine cluster medium; inner ramus posteriorly setose; outer ramus narrow, apex sub-acute. Uropod 3, outer ramus slightly the longer, terminal segment medium; inner ramus lacking inner marginal setae. Telson lobes short, broad, with few dorso-distal setae.

**Distribution.** A southern species, abundant along coasts of California and Oregon, diminishing in Washington, and barely entering British Columbia. Occurs along outer surf-exposed sand beaches, from MLW to shallow subtidally.

**Taxonomic Commentary.** The large female specimen from Jordan R. exhibited a very broad segment 6, and heavy facial spines on segments 4 & 5 of peraeopods 5 and 6.

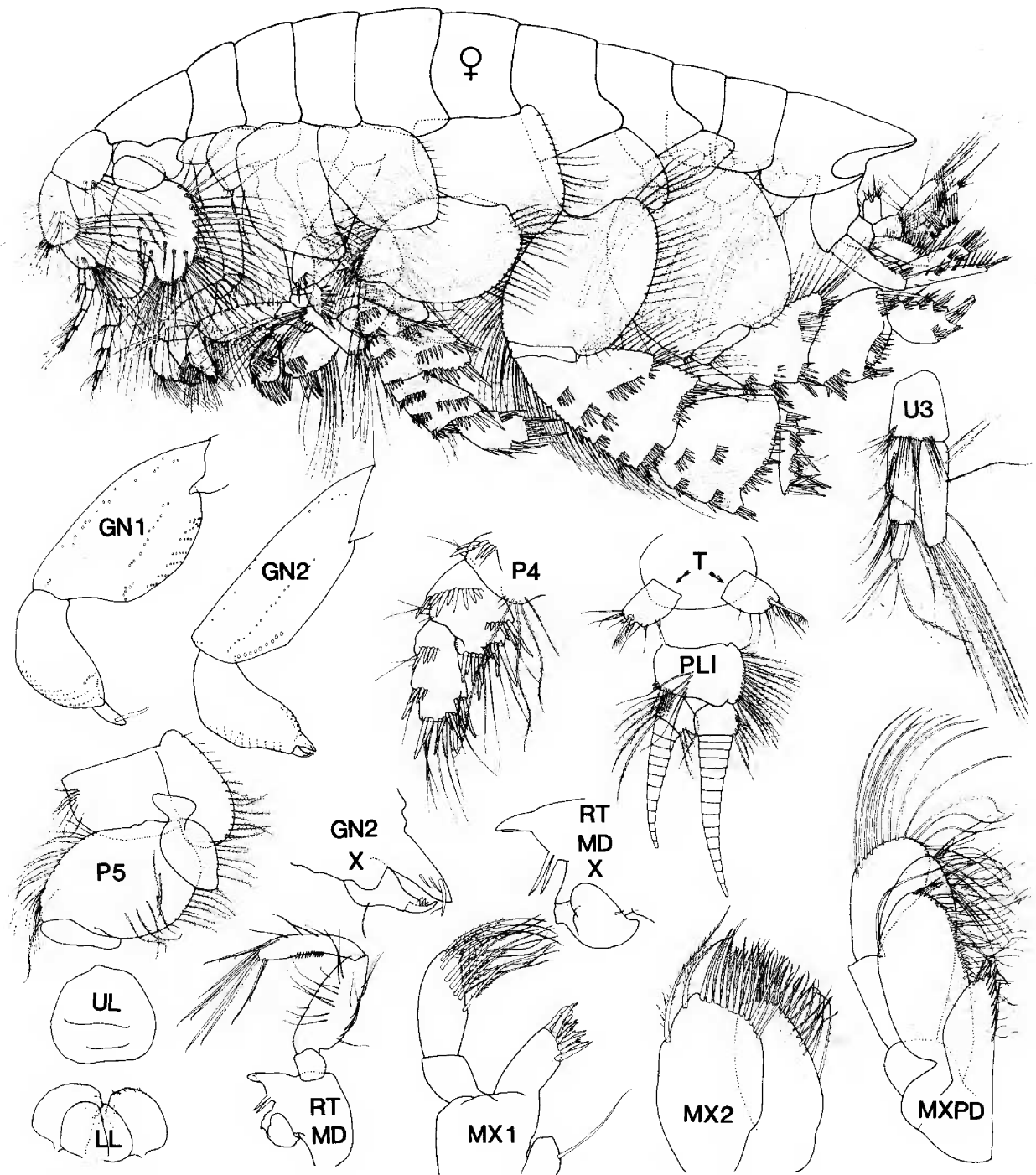
*Eohaustorius sencillus* J. L. Barnard  
(Fig. 7)

*Eohaustorius sencillus* Barnard, 1962: 249, figs 1, 2.—Bosworth, 1973: 8 (key).—Barnard, 1975, fig. 44.—Barnard & Karaman, 1991: 363.

**Material examined.** Mile buoy, off Moss Landing, California, 20 m sand, P. Slattery coll., Feb. 24, 1971 - 1 female (slide mount) (**figured specimen**), CMN Cat. no. NMCC1991-1241; 13 additional females, 2 males.

**Diagnosis.** Female (3.5 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, peduncular segment 2, anterior margin weakly setose, bare proximally. Antenna 2, peduncular segment 4 relatively short and deep, postero-distal lobe medium, hind margin with 25-30 plumose setae; segment 5 as deep as long; basal flagellar segment postero-distally with 4-5 long setae.

Mandible, palp segment 3 slender, with 7 posterior marginal comb spines. Maxillae undescribed. Maxilliped, outer plate broad; palp segment 2, medial lobe large, broad, shorter than moderately broadened terminal segment.



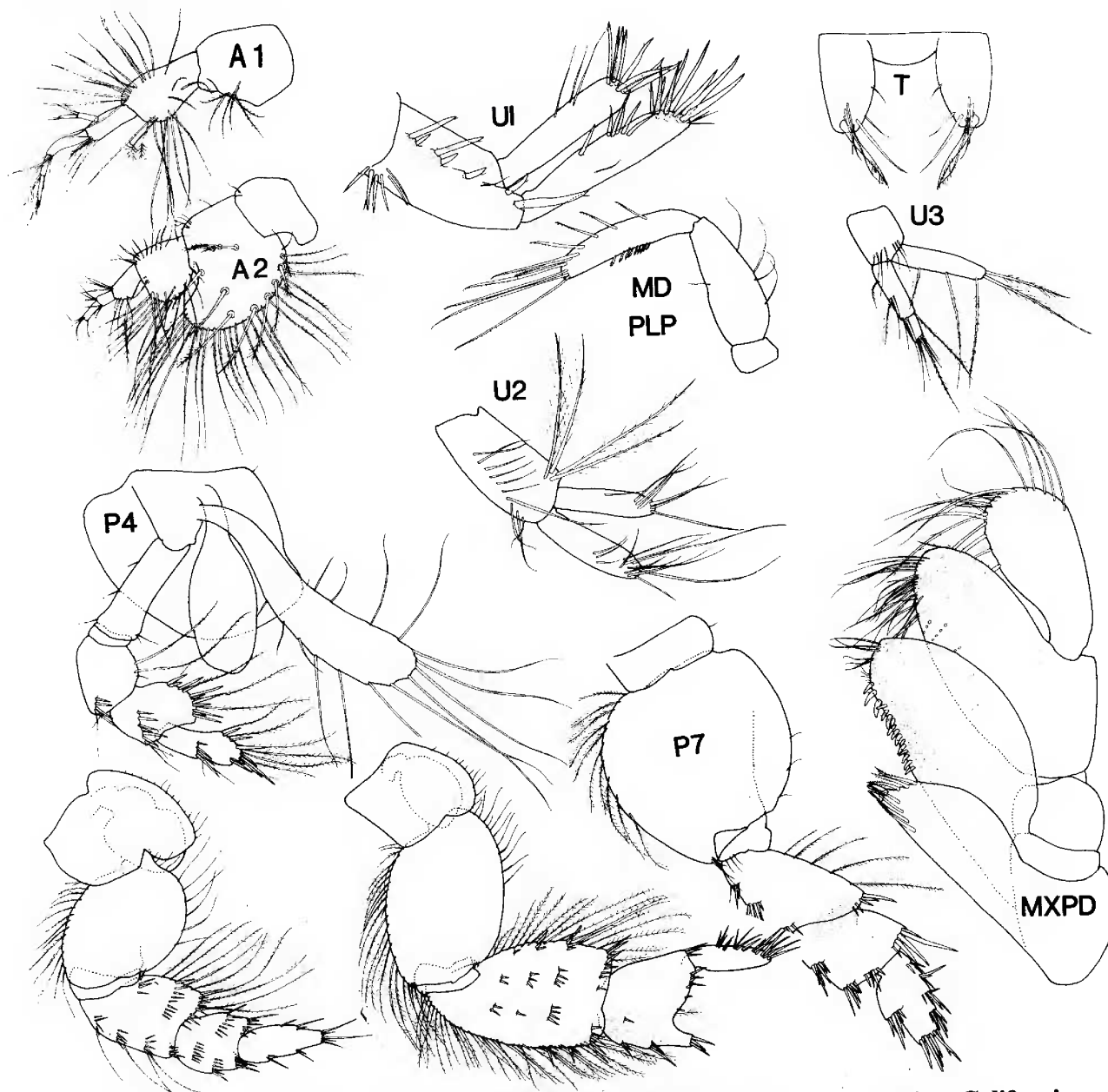
**FIG. 6. *Eohaustorius sawyeri* Bosworth, 1973. Female ov ( 3.2 mm). Off Long Beach, V.I., B.C.**

Coxae 1 & 2 squarish below. Gnathopod 1, basis with 7-8 posterior marginal setae; segment 5 medium, deep, convex below; segment 6 sharply broadest medially; dactyl, unguis large, heavy. Gnathopod 2, basis lined posteriorly with longish setae; segment 5 slender, strongly setose; postero-distal spines few, weak; segment 6 slender, regular.

Peraeopod 3, coxa deep, sublunate; segment 4 medium broad distally, hind margin with 7-9 setae; segment 5 relatively shallow, anterior margin bare, not emarginate proximally, lower margin proximally setose; segment 6 lenticular,

margins slender spinose. Peraeopod 4, segment 4 relatively large, hind margin convex, with 2-3 long setae, anterior margin with weak oblique spine row; segment 5, with weak anterior oblique spine row, posterior lobe medium, rounded behind, with 2 weak postero-proximal spine groups; segment 6 slender, with anterior marginal spine cluster, and 2 postero-distal single marginal spines.

Peraeopod 5, basis ovate, hind margin lacking distal setae; segment 4 not broader than deep, parallel-sided, facial spine groups weak; segment 4 relatively small, not wider



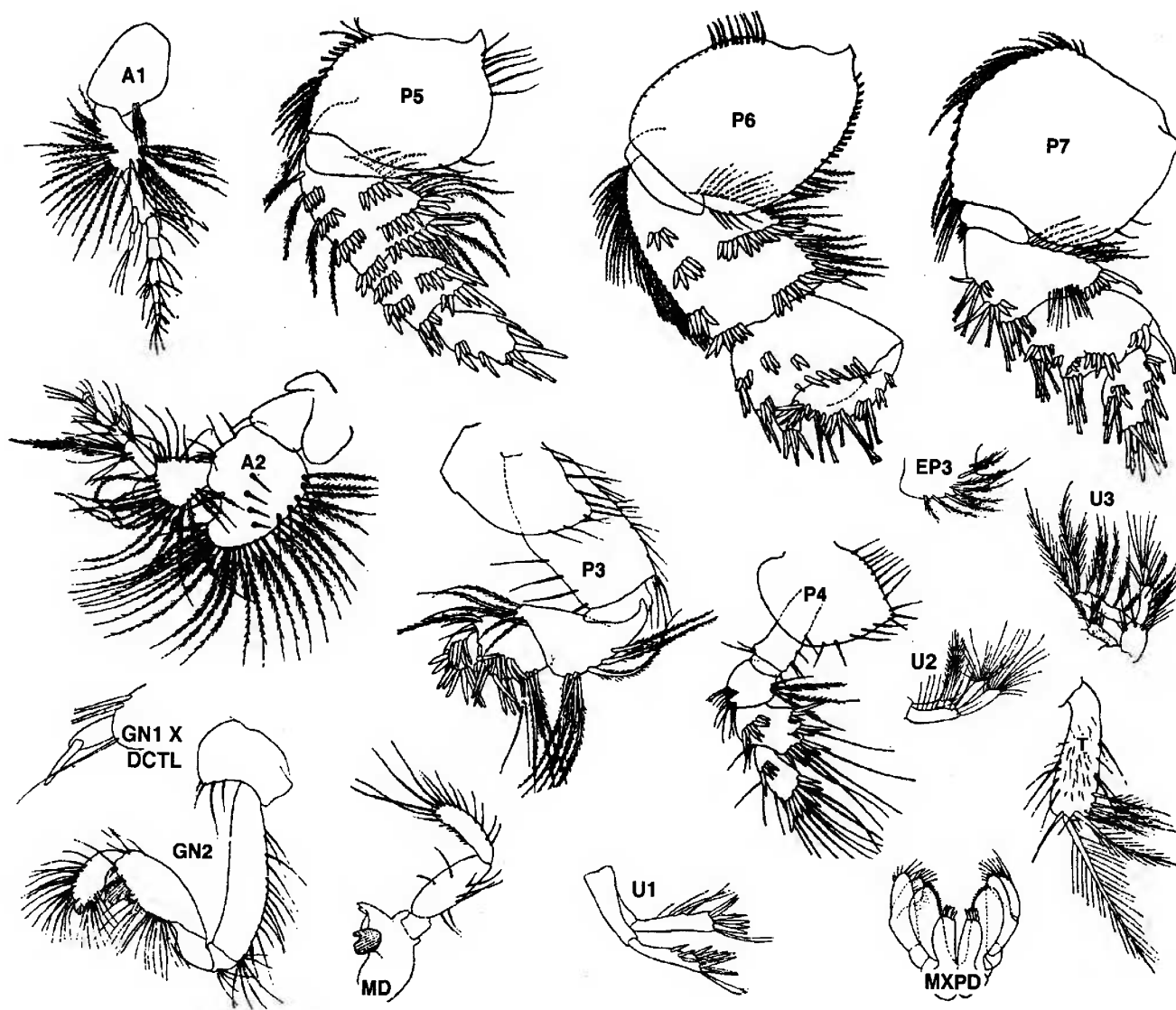
**FIG. 7. *Eohaustorius sencillus* Barnard, 1962. Female (3.5 mm). Off Moss Landing, California.**

than deep, facial spine groups weak; segment 6 not broadened, anterior and posterior margins each with 2 single slender spines, apex narrowly truncate, weakly spinose. Peraeopod 6, coxa narrow, deep; basis relatively little broadened, hind margin with proximal setae only; segment 4 elongate, broadest medially, with 6 small facial spine clusters; segment 5 not broader than deep, with single facial spine; antero-distal margin with 4-5 spines, excavation deep; segment 6 regular, hind margin with 4-5 clusters of slender spines. Peraeopod 7, basis large, medium broad, subovate, hind margin virtually bare, lacking proximal cusp; segment 4 longer than broad, gently broadening distally, anterior margin with 2 spine clusters, hind margin with 5 plumose setae; segment 6 slightly broader than deep, with anterior spine cluster; anterior distal free margin relatively short; segment 6 medium broad, anterior margin with 1, posterior margin with 3-4 spine clusters, apex truncate, spinose.

Pleon plate 3, hind corner acutely produced, short, tip directly beneath dorsal hind process. Uropod 1, peduncle, outer margin nearly bare, distal spine cluster weak; inner ramus weakly setose posteriorly; outer ramus, posterior margin with slender spines. Uropod 3, rami subequal, length ~2X peduncle; outer ramus, terminal segment very short (<1/3 proximal segment); inner ramus, hind margin nearly bare. Telson lobes short, broad, with 6-8 dorso-distal setae.

**Distribution.** From Pt. Conception north through California to Southern Oregon (Bosworth), subtidally to 20 m; not reaching Canadian waters.

**Taxonomic Commentary.** This species is distinguished by the relatively large basis of peraeopod 7, and large dactyl of gnathopod 1. Bosworth (pers. communic.) recognized a variant in deeper water material of J. L. Barnard (loc. cit.).



**FIG. 8.** *Eohaustorius gurjanovae*, new species. Female ov (6.0 mm). Southern Sakhalin I., Sea of Japan. (modified from Gurjanova, 1962)

*Eohaustorius gurjanovae*, new species  
(Fig. 8)

*Eohaustorius washingtonianus* Gurjanova, 1962: 404, figs. 135B, V.

**Type material.** Female ov (6.0 mm), **Holotype**; 7 females and males, **Paratypes**, from south coast of Sakhalin I., Sea of Japan; collections of the Zoological Museum, St. Petersburg, Russia.

**Diagnosis.** Female (7.0 mm): Head, rostrum short; pigmented eyes lacking. Antenna 1, peduncle 2 anteriorly setose throughout. Antenna 2, peduncular segment 4, posterior margin with 25-30 plumose setae; postero-distal lobe large, extending to mid-point of deep segment 5; basal flagellar segment with 1 stout postero-distal plumose seta.

Mandibular palp medium, with 7-8 posterior marginal

comb-spines. Maxillae 1 & 2 undescribed. Maxilliped, outer plate slender, tall; palp segment 2, inner lobe slender, long, nearly reaching tip of clavate palp segment 3.

Gnathopod 1, coxa, hind corner squarish; dactyl, body palm-shaped, unguis large. Gnathopod 2, basis, posterior margin lined with medium setae; segment 5 slender, postero-distal spine cluster strong; segment 6 much shorter, slender.

Peraeopod 3, coxa, anterior margin rounded; basis thick, heavy; segment 4 short, expanding to broad distal margin, antero-distal angle and posterior margin with several plumose setae. Peraeopod 4, coxa subquadrate, lower and hind margins setose; basis with a few postero-distal setae; segment 4, hind margin with 3-4 plumose setae, anterior margin with medial cluster of slender spines; segment 5 hind lobe short, anterior margin with oblique row of stout spines, postero-proximal margin with 2 groups of stout spines; segment 6 short, broadening distally to large apical cluster of spines, anterior margin with single spine cluster and a few setae.

Peraeopod 5, basis broad, orbicular, hind margin devoid of setae except proximally and mid-distally; segment 4 broadening gradually, longer than wide, with clusters of stout facial spines; segment 5 smaller and narrower, facial spines strong; segment 6 broad, anterior margin with 2 clusters of stout spines, posterior margin with 2 singly inserted spines, apical spines strong. Peraeopod 6, basis medium broad, hind margin setose throughout, except for short distal gap; segment 4 short, very broad, with 2 anterior clusters and 1 posterior submarginal row of stout spines; segment 5 much broader than deep, with 2 facial spine clusters, and 6-7 antero-distal marginal spines, distal excavation medium deep; segment 6 large, bent forward, hind margin with 6 clusters of spines, some elongate distally. Peraeopod 7, basis very broad, hind margin with 4-5 medio-distal setae and blunt proximal cusp; segment 4 broadly triangular, anterior margin with 2 spine clusters, hind margin setose throughout; segment 5 large, slightly broader than segment 4, anterior margin with 2 spine clusters, antero-distal free margin heavily spinose, postero-distally angle with medium stout spine; segment 6 medium, anterior margin with 3-4, and posterior margin with 3, spine clusters, some spines elongate, apex broad, heavily spinose. Long anterior marginal spines are split-tipped or clavate.

Pleon plate 3, hind corner normally produced, acute, not elongate, with several lower marginal and submarginal plumose setae. Uropod 1, peduncle, outer margin weakly or not spinose; outer ramus, posterior margin with subapical fan of spines; inner ramus, posterior margin distally with long setae. Uropod 2, peduncle and rami regularly setose. Uropod 3, rami subequal, shorter than 2X peduncle; terminal segment of outer ramus short; inner ramus with 4-5 inner marginal setae. Telson lobes slender, each with 5-6 dorso-distal plumose setae and several inner marginal fine setae.

**Etymology.** The species is named in honour of the late Eupraxie F. Gurjanova who first recorded and figured the material from the Soviet far eastern region, as reproduced here.

**Distribution.** South coast of southern Sakhalin I., Sea of Japan, in sand at 19 m. depth.

**Taxonomic commentary.** *E. gurjanovae* is another member of the advanced group of species including *E. robustus*, *E. cheliferus* and *E. washingtonianus*. As noted by Dr Gurjanova (loc. cit., p. 405), this species differs from the North American Pacific species, *E. washingtonianus*, in a number of morphological character states, including the stronger armature of peraeopods 5-7, the more numerous carpal spines of gnathopod 2, and the linear setose lobes of the telson. Together these two forms do not qualify as a pan-Pacific sibling species pair and are here considered distinctly separate species.

*Eohaustorius robustus* (Gurjanova) new status  
(Fig. 9)

*Haustorius eous robustus* Gurjanova, 1953:216.

*Eohaustorius robustus eous* Gurjanova, 1962:409.—Barnard & Karaman: 363.

**Material examined.** No specimens were taken in the North American study region.

**Diagnosis.** Female (6.5 mm): Head, rostrum short. Pigmented eyes lacking. Antenna 1, flagellum short, peduncular segment 2 with thick, coarse, facial plumose seta distally. Antenna 2, peduncular segment 4 short and deep, hind margin with ~35 plumose setae; postero-distal lobe large; segment 5 deepest mid-distally; basal flagellar segment postero-distally with 3 short plumose setae.

Mandibular palp, segment 3 relatively broad, shorter than 2 relatively, with 7 posterior marginal comb spines. Maxillae and maxillipeds not described or figured.

Coxae 1 & 2 small, regular. Gnathopod 1, basis, hind margin sparsely setose; segment 5 large, deep, strongly setose behind; segment 6 short broad; dactyl with long straight unguis. Gnathopod 2, basis, hind margin with several long setae; segment 5 elongate, postero-distal spines numerous, short, apically spoon-shaped; segment 6 short, apically narrowing abruptly.

Peraeopod 3, coxa rectangular, basis, hind margin setose throughout; segment 4 broadening gently distally, hind margin setose throughout; segment 5, anterior margin with proximal excavation or notch, hind margin proximally with plumose setae; segment 6 lenticular, marginal spines strong. Peraeopod 4, coxa rounded anteriorly, with squared hind corner; basis with antero- and postero-distal clusters of setae; segment 4, hind margin with 5 setae, 3 longish; segment 5, anterior margin with single setal cluster, hind lobe medium, antero-distal spine cluster strong, distal margin bare; segment 6 small, short, with hind margin and apical spine clusters.

Peraeopod 5, coxa deep, hind margin strongly setose; basis asymmetrically broad, hind margin distally bare; segment 4 broadening distally, with strong marginal and facial spine clusters, and strong postero-distal setal cluster; segment 5 narrower, squarish, with stout spine clusters; segment 6 medium, with 1 anterior marginal spine cluster, and a few posterior marginal and apical spines. Peraeopod 6, basis relatively short and very broad, broadest distally, hind margin short-setose; basis large, broadening distally, with strong anterior facial clusters and posterior facial row of spines; segment 5 broadest distally with 2 strong anterior facial spine clusters; antero-distal margin with 9-10 spines, excavation deep; segment 6 large, bent forward, hind margin with 5 spine clusters, some distal spines elongate, tips funnel shaped, notched. Peraeopod 7, basis very broad, proximally truncate

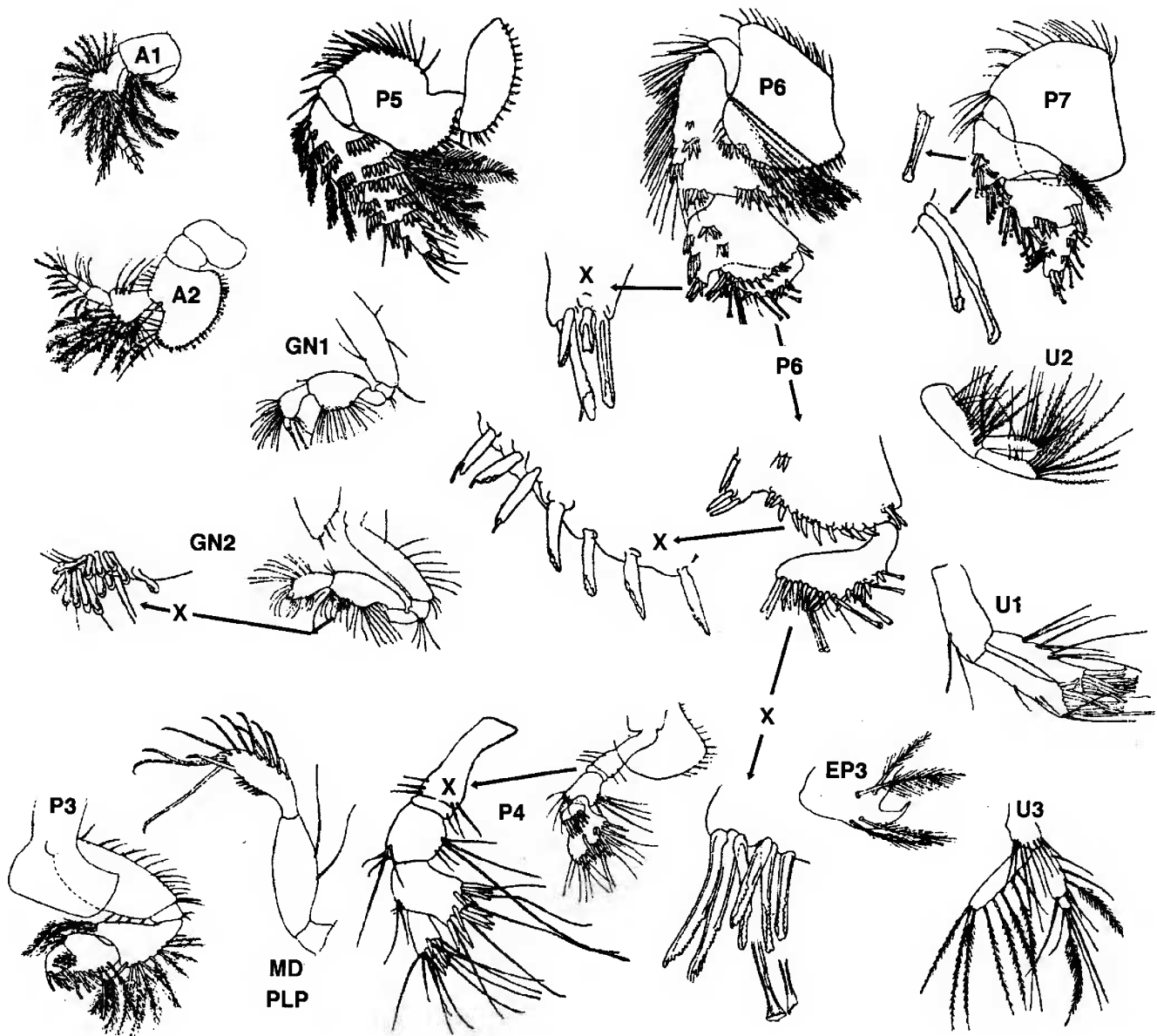


FIG. 9. *Eohaustorius robustus* (Gurjanova). Female (7.0 mm). Greater Kurile Islands. (modified from Gurjanova, 1962).

behind, margin smooth; segment 4 short, very broad, hind lobe narrow, with apical cluster of plumose setae; segment 6 short, very broad, with 2-3 anterior marginal, and 3 posterior marginal spine groups. Longest anterior marginal spines of segments 4-6 are club- or funnel-tipped.

Pleon side plate 3 with a few facial and submarginal plumose setae; hind corner moderately produced, acute, apex upturned slightly. Uropod 1, rami and peduncle subequal, both rami with distally hooked apical spines; outer ramus with weak subapical setae, inner ramus, posterior margin with 3 groups of long setae. Uropod 2 rami shorter than peduncle, normally setose. Uropod 3, rami short, less than 2X peduncle; terminal segment of outer ramus very short (1/4 proximal segment); inner ramus, inner margin with 5-6 stout plumose setae.

Telson lobes medium, narrowing distally, with about 7 dorso-distal setae.

**Distribution.** Pacific coast of the Large Kurile Island chain (Paramushir, Iterup Islands), and sublittoral of the northwestern Sea of Okhotsk, at depths of 10-40 m.

**Taxonomic commentary.** Another species of the advanced subgroup (including *E. cheliferus*), but distinguished by characters given in the key (p. 37). It is not at all closely related to *E. eous*, from which it is distinguished by a combination of 3-4 species level character states. *E. robustus* is superficially close to *E. gurjanovae* in several character states of pereopods 5-7.

*Eohaustorius brevicuspis*, Bosworth  
(Fig. 10)

*Eohaustorius brevicuspis* Bosworth, 1973: 255, figs. 1-3.  
—Austin, 1985: 605.—Staudé, 1987: 383, 372 (key).—  
Barnard & Karaman, 1991: 363.

**Material examined.** 4 lots containing 20 specimens,  
none from British Columbia.

WASHINGTON.

ELB Stn W39, Neah Bay, Clallam Co., medium sand at LW,  
July 30, 1966 - 3 males, 2 females, 1 im. NMCC1991-1233;  
ELB Stn. W46, Leadbetter Pt., Pacific Co., surf exposed sand  
at LW, Aug. 4, 1966 - 4 males, 2 females, NMCC1991-1236.

OREGON.

ELB Stn. W58, Seal Rock, Lincoln Co., LW surf sand, Aug.  
13, 1966 - 1 female ov (4.5 mm) (slide mount) (**figured  
speci-men**), 1 female ov (4.6 mm) slide mount, CMN Cat.  
no. NMCC1991-1237; 4 males, 5 imm.

CALIFORNIA.

ELB Stn. C1, Crescent City, surf sand beach at LW - 1  
subadult female, NMCC1991-2094.

**Diagnosis.** Female ov (4.0 mm): Head, rostrum short,  
blunt, not exceeding antero-lateral head lobes. Eyes small  
ovate, adjacent to anterior margin, whitish, lacking pigment.  
Antenna 1, peduncular segment 2 with strong anterior margin-  
clusters of setae. Antenna 2, peduncular segment 4  
short, medium deep, hind margin with relatively few (18-20)  
plumose setae, postero-distal lobe short; segment 5 little  
broadened distally.

Mandible, palp segment 3 medium long, with 12 poste-  
rior marginal comb spines. Maxilla 1 & ??? Maxilliped,  
outer plate medium; palp segment 2, inner lobe relatively  
small, distinctly exceeded by broadly expanded palp seg-  
ment 3.

Coxa 1?, coxa 2 rounded below. Gnathopod 1, basis,  
anterior margin proximally with short setae, posterior margin  
distally with a few long setae; segment 5 long, deep;  
segment 6 short, distally slightly broadening. Gnathopod 2,  
basis, anterior margin medially setose, posterior margin with  
a few longish setae; segment 4 slender, shallow; segment 6  
short, not medially broadened.

Peraeopod 3, basis, anterior and posterior margins distally  
with a few long setae; basis medium broad distally, hind  
margin sparsely plumose-setose, segment 5 shallow, with  
postero-proximal marginal setae; segment 6 small, lenticular,  
margins spinose. Peraeopod 4, coxa very broad, lower  
margin nearly straight; segment 4, anterior margin with 2  
small groups of setae, hind margin with pair of long plumose  
setae; segment 5, anterior marginal oblique spine row strong,  
posterior lobe medium, hind margin proximally with a few  
spines and setae, distal margin with weak spine cluster;  
segment 6 medium, anterior margin with 2 weak clusters of

spines and setae, hind margin distally to apex with a few  
longish setae and medium spines.

Peraeopod 5, coxa shallow, hind lobe, lower margin  
setose; basis broader than deep, hind margin setose through-  
out; segment 4 slightly broadening distally, anterior clusters  
and posterior rows of facial spines strong; segment 5 slightly  
narrower, facial spines strong; segment 6 medium, with 2  
anterior marginal spine clusters, posterior margin with single  
spines. Peraeopod 6, basis broadening distally, with large  
postero-distal lobe, hind margin setose proximally; segment  
4 very broad distally, with 2 weak facial spine groups;  
segment 5 short, very broad with 1 posterior and 2 anterior  
submarginal facial spine groups, distal margin with 6-7  
spines, distal excavation medium; segment 6, short, thick,  
posterior margin with 6-7 spine clusters, long spines split-  
tipped. Peraeopod 7, basis very broad, suborbicular, hind  
margin nearly bare, with broadly rounded proximal cusp;  
segment 4 short very broad distally, anterior margin with 3  
spine clusters, posterior margin with a few plumose setae  
distally; segment 5 narrower, but wider than long, anterior  
margin with 2-3 spine clusters, postero-distal corner with  
short to medium spines; segment 6 broad, with 1 anterior and  
2 posterior marginal spine clusters and long spines at trun-  
cate apex.

Pleon plate 3, hind corner moderately strongly produced,  
tip acute, not upturned. Uropod 1, peduncle, outer margin  
with a few distal spines and apical cluster of 3 heavy spines;  
rami with strong apical spine clusters; inner ramus with  
several long posterior marginal setae and a medio-distal  
cluster of spines; outer ramus with a few posterior marginal  
spines; uropod 3, rami subequal, ~2X peduncle, terminal  
segment of outer ramus medium; inner ramus, inner margin  
with 3-4 plumose setae.

Telson lobes short, thick, with 7-8 dorsal distal setae and  
several inner marginal setae.

**Distribution.** Central California north to the Strait of  
Juan de Fuca, in clean medium sand of surf exposed high  
salinity beaches, MW level to immediate subtidal depths.

**Taxonomic commentary.** *E. brevicuspis* is closely  
similar to the intertidal species *washingtonianus*, overlap-  
ping it distributionally in the Oregon-Washington region, and  
replacing it further south.

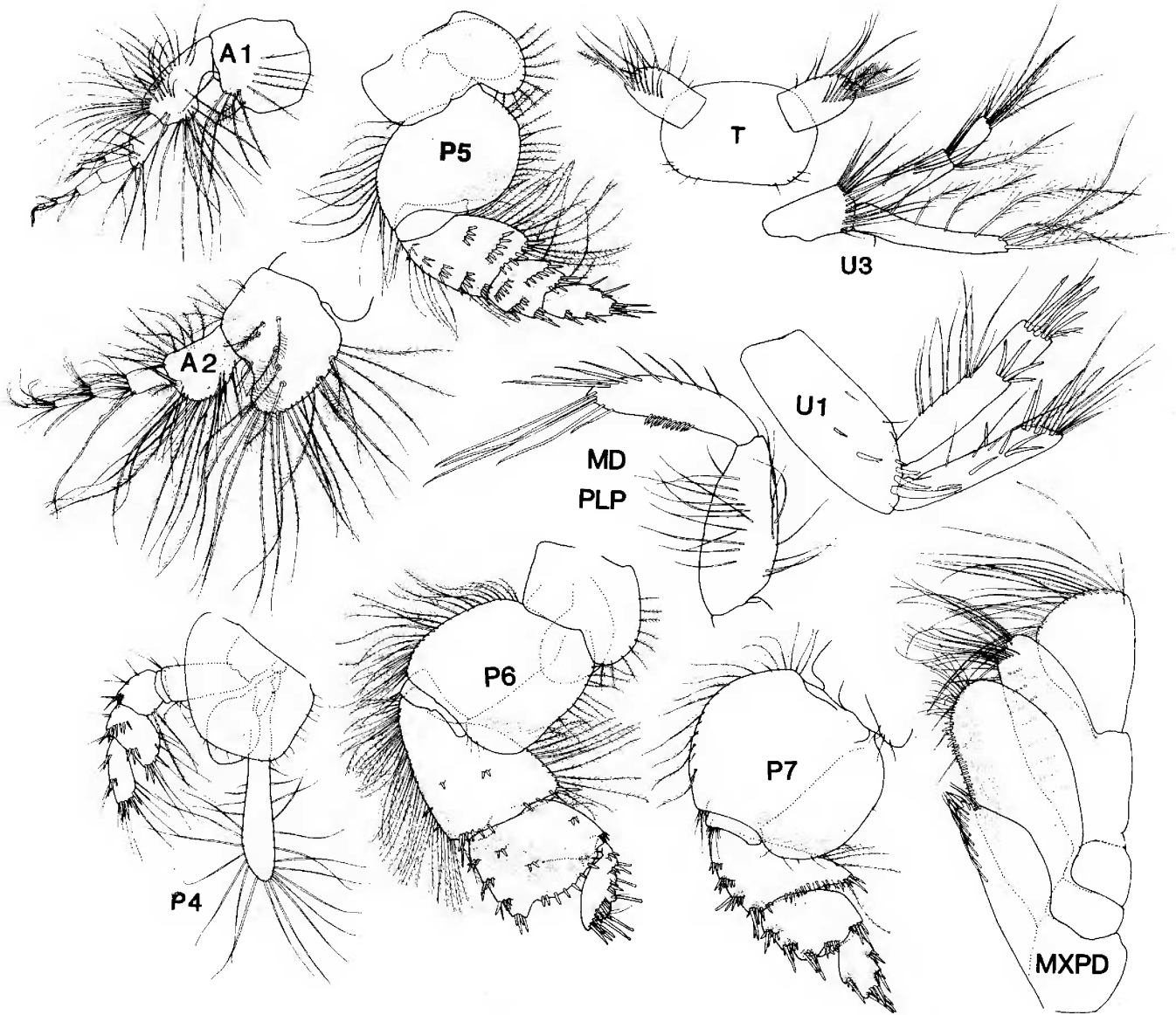
*Eohaustorius washingtonianus* (Thorsteinson)  
(Figs. 11, 12)

*Haustorius washingtonianus* Thorsteinson, 1941: 61, figs.  
39-51.

*Eohaustorius washingtonianus* J.L. Barnard, 1957: 81(part).  
—Barnard, 1962: 249 (key).—Bosworth, 1973: 8 (key), fig.  
E.—Austin, 1985: 607.—Staudé, 1987: 383, 372 (key).—  
Barnard & Karaman 1991: 363.

**non:** *Eohaustorius washingtonianus* Barnard, 1957: Pl. 16.  
—Gurjanova, 1962: fig. 135A.





**FIG. 10. *Eohaustorius brevicuspis* Bosworth, 1973. Female ov (4.5 mm). Seal Rock, Oregon.**

**Material examined.** About 55 lots containing approx. 600 specimens, of all sexes and life stages (except very juvenile), as follows (numbers of specimens in parentheses):

**SOUTHEASTERN ALASKA.**

Prince William Sound to Alexander Archipelago, ELB stns., June-Aug., 1961, LW and shallow sub-tidal levels - A54 (3); A71 (1); A81 (30); A83 (1); A121 (1); A140 (1). ELB Stns, July 28 - Aug. 4, 1980: S4B1 (1); S4B2 (f.w. stream outflow) (2); S11B3 (15); S16B1 (1); S16B4 (2); S19B1 (2); S16B4 (2).

**BRITISH COLUMBIA.**

Queen Charlotte Islands, ELB Stns, July-August, 1957: H3 (1); H8a (2); H13 (29); H14 (17); E1 (12); E14b (31); E17 (4); E21 (1); W2 (44).

North-central mainland coast, ELB Stns, July, 1964: H1 (3); H10 (11); H23 (48); H39 (15); H48 (32); H50 (49); H59 (3).

Northern Vancouver I. & adjacent mainland: ELB Stns, 1959: N1 (15); N6 (16); O13 (1).

Central Vancouver I., ELB Stns 1975: P28 (48); P29 (1). Southern Vancouver I., ELB Stns., 1955: F4, Albert Head, near Victoria (2); F5 (9); P6a (8); P8 (4). ELB Stns., July, 1970: P703 (4); P708 (22); P711 (17); P716 (5); P17 (1). ELB Stns., 1964: H41 (16); H42 (16); H43 (79); H45 (25). ELB Stns., 1975: P1c(15); P1b (46). ELB Stns., 1976: B12a (2); ELB Stns, 1977: B5a, Witty's lagoon - 1 female ov (7.0 mm), female ov (5.0 mm), male (5.0 mm) (slide mounts), + 14 additional females, CMN Cat. no. NMCC1991-2107; B5c (51).

Southern mainland, ELB Stns., 1955: M11, White Rock (10).

**WASHINGTON**

ELB stations, 1966: W34, Crescent Beach, LW sand (with *E. estuarius*) - 10 males, 19 females, 5 im.

**Diagnosis.** Female (5.0 mm): Head, rostrum short. Eyes small, lenticular, whitish, lacking pigment. Antenna 1, segment 2 with strong anterior marginal setae, lacking proximally. Antenna 2, segment 4 medium deep, hind margin with ~25 plumose setae, postero-distal lobe medium; segment 5 large, medium broad; flagellar segment 1 with single postero-distal plumose seta.

Mandible, palp segment 3 medium, with 11-12 posterior marginal comb spines. Maxilla 1, palp segment 1 short. Maxilla 2, inner plate with inner marginal setae only. Maxilliped, inner plate and outer plates broad; palp segment 2, medial lobe broad, not attaining tip of moderately broadened segment 3.

Coxa 1, and 2 small, squarish. Gnathopod 1, basis with few distal posterior marginal setae; segment 5 medium deep; segment 6 broadening distally. Gnathopod 2, basis with postero-distal marginal setae; carpus slender, elongate, postero-distal spines slender; segment 6 short, medially broadest.

Peraeopod 3, basis medium, hind margin with distal setae; segment 4 long, gently broadening distally; segment 5 medium deep, anterior margin with shallow proximal excavation, hind margin proximally with setae; segment 6 drop-shaped, margins slender-spinose. Peraeopod 4, segment 6, hind margin with 2-3 long plumose setae; segment 4 with strong anterior marginal oblique row of spines, hind lobe medium, with 2 postero-proximal, and 1 distal, spine cluster; segment 6 slender, with 2 anterior groups of spines and setae, and hind margin distally with single spines and setae.

Peraeopod 5, coxa, hind lobe deep, margin weakly setose; basis short broad, suborbicular, hind margin setose except distally; segment 4 short, broadest distally, with moderate anterior clusters and posterior rows of facial spines; segment 5 longer than wide, facial spines strong; segment 6 slender, with 2 anterior marginal and 3 posterior marginal clusters of slender spines and setae, apex slender-spinose. Peraeopod 6, coxa deep, hind lobe setose below; basis broad, with shallow distal lobe, hind margin setose proximally; segment 4 medium long, broadest distally, with 2 weak facial spine clusters; segment 5 broadest distally, with 2 medium posterior facial clusters of spines and distal marginal row of 8-10 spines, distal excavation medium; segment 6 medium, nearly straight, hind margin with 5-6 clusters of spines, a few distal spines long, split-tipped. Peraeopod 7, basis broad, suborbicular, hind margin nearly bare, with strong proximal cusp or tooth; segment 4 medium, widest distally, hind margin setose throughout; segment 5, anterior margin with 2 clusters of spines, tips clavate, distal free margin with small spine cluster; segment 6 medium broad, with 1 antero-marginal and 2 postero-marginal clusters of spines.

Pleon plate 3, hind corner weakly produced, acute, well exceeded by postero-dorsal pleosomal lobe. Uropod 1, peduncle with a few weak marginal spines, distally with 3-4 stout spines; rami subequal; inner ramus, posterior margin setose; outer ramus posteriorly with singly inserted and clusters of spines and setae. Uropod 3, outer ramus, terminal

segment medium; inner ramus with 4-5 inner marginal plumose setae. Telson lobes short, thick, with 5-6 dorso-distal and 4-5 inner marginal setae.

**Distribution:** From Prince William Sound, Alaska, southward along southeastern Alaska, British Columbia and Washington to southern Oregon, possibly to central California. It occurs bathymetrically from about mid-tide to shallow sub-tidal levels, in fine sand, mainly along open, surf-exposed beaches, but also on protected beaches; it co-occurs with *E. estuarius* in salinities as low as ~ 10‰.

**Taxonomic commentary:** *E. washingtonianus* is the type of a unique and moderately advanced N. American endemic group of species. It contains 3 other N. American endemic full species, as noted in the key, and a variety as noted below. The group is typical of high energy intertidal surf sands, but the subtidal members are less strongly armoured. This species complex is most closely related to *E. eous* group of western Pacific shores. As noted by Gurjanova (1962), it bears some resemblance to, and possible direct relationship with, *E. gurjanovae* (see histogram, p. 59).

#### *Eohaustorius washingtonianus* variant

##### Material examined.

##### BRITISH COLUMBIA.

North-central coast. ELB Stns., 1964: H48, Goose I., north beach, fine sand at LW level, 9.8 C., Aug. 5 - 17 males, 14 females, 1 immature. ELB Stns., 1959: N1, Open Bight, Rivers Inlet, coarse sand at LW level, Aug. 3 - 15 im., CMN Cat. no. NMCC1991-2095; N6, Bremner Beach, near Raynor Pt., fine sand at LW level, 10.0 C., Aug. 6 - 7 males, 9 females.

**Taxonomic commentary.** Bosworth (personal communication) briefly commented upon a somewhat anomalous feature of specimens of "*washingtonianus*" from the three stations listed above. This observation is here confirmed. In peraeopod 7, segment 2 (basis) bears a small but distinct postero-proximal cusp, typical of *E. washingtonianus*, *E. brevicuspis* and *E. barnardi* of North American beaches, and *E. gurjanovae* of western Pacific shores (p. 47). However, the present variant resembles *E. barnardi* in having a single group of spines (excluding the antero-distal group) on the anterior margin of segment 5 of peraeopod 7. This northern variant differs from *E. barnardi* in its other specific characters (key, p. 37), but appears otherwise similar to material of *washingtonianus* from adjacent northern localities. We therefore conclude, tentatively, and on the basis of the limited material available, that specimens from the three stations above represent a local, mainly subtidal, variant of the typical form of *Eohaustorius washingtonianus* (Thorsteinson).

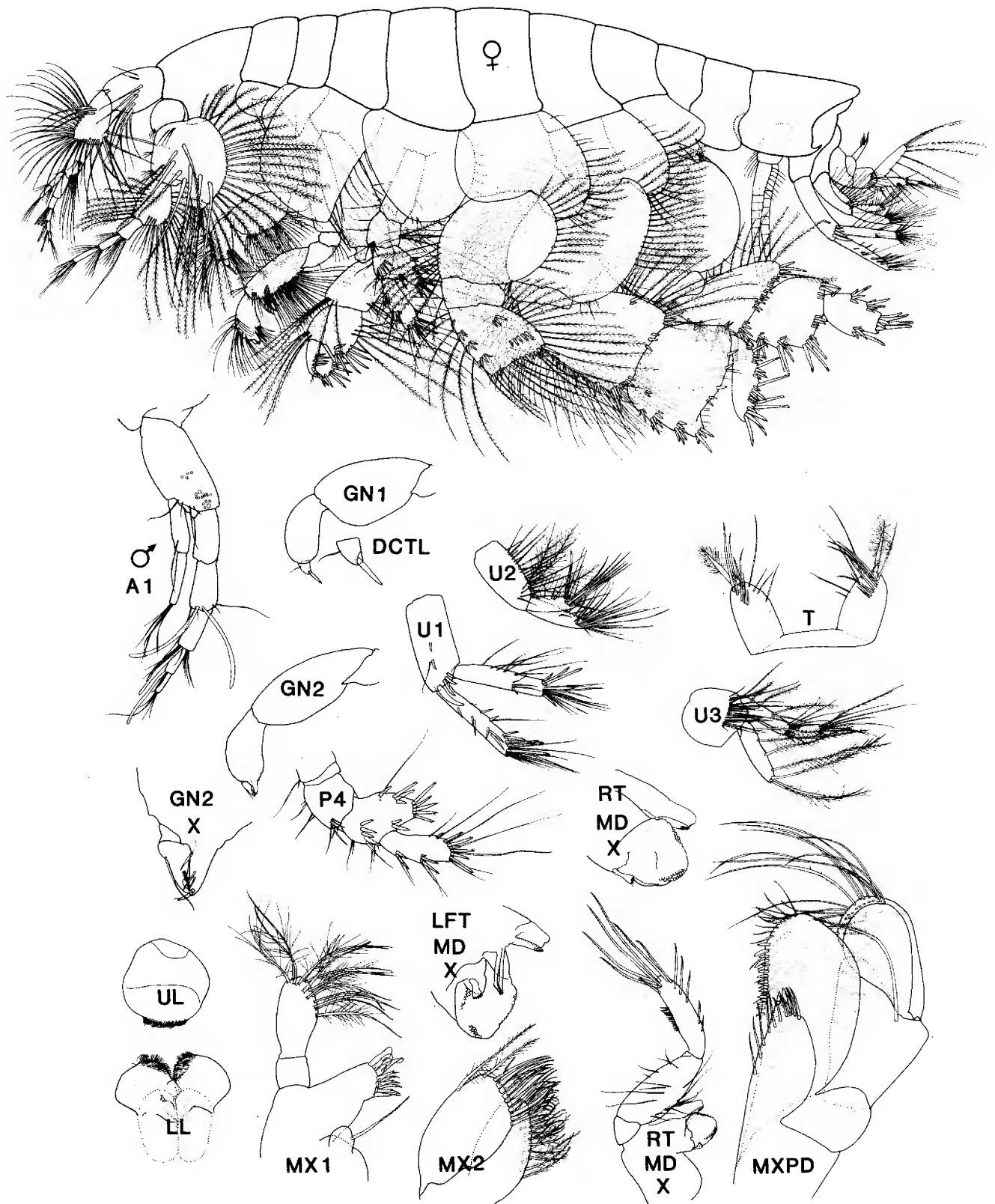


FIG. 11. *Eohaustorius washingtonianus* (Thorsteinson). Female (5.5 mm). Pt. Roberts, WA.

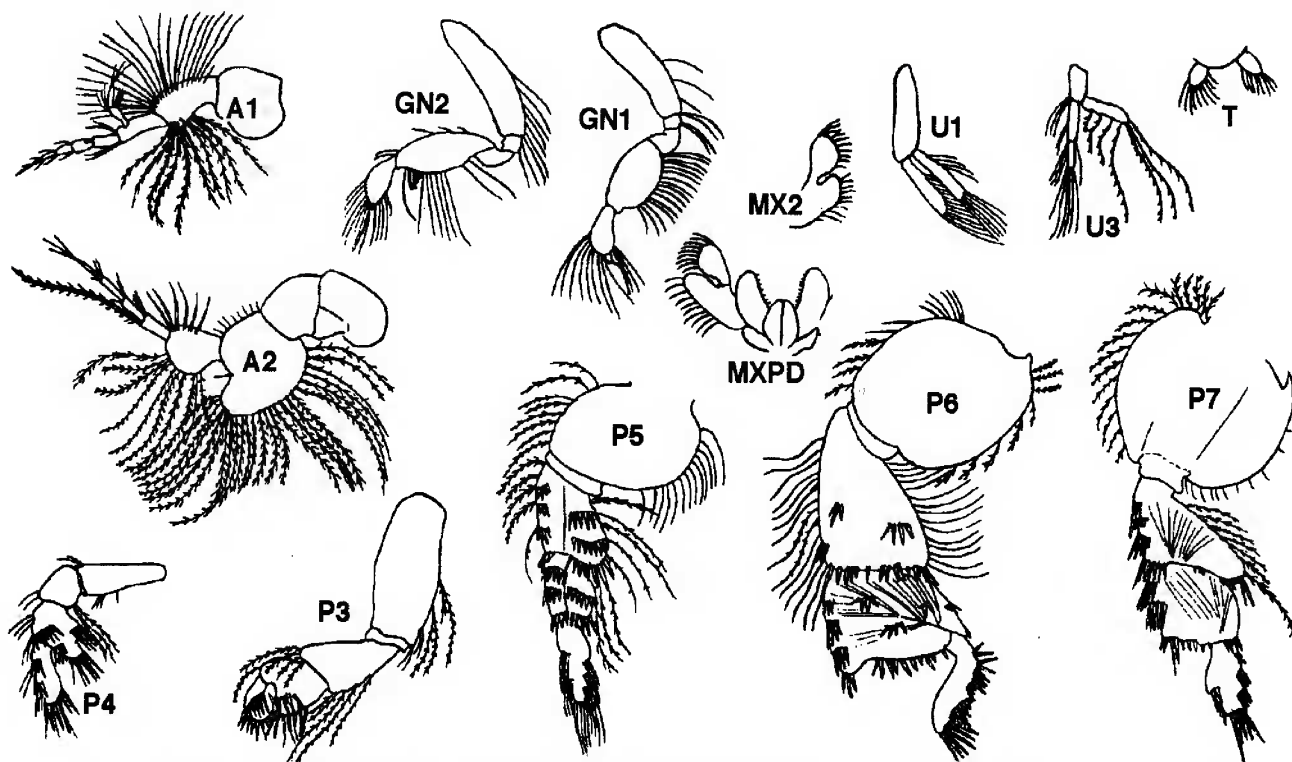


FIG. 12. *Eohaustorius washingtonianus* (Thorsteinson). Female (5.5 mm). Point Roberts, WA. (after Thorsteinson, 1941).

*Eohaustorius barnardi*, new species  
(Fig. 13)

*Eohaustorius washingtonianus* J. L. Barnard, 1957: 82, plate 16.—Bosworth, 1974 (letter and manuscript to ELB).

**Material.** The species occurred in samples from the 1956 and 1959 "Velero" cruises near Pt. Conception, and further south, in depths of 5-20 meters (Barnard, loc. cit.).

The species was also collected by E. W. Fager from the end of the Scripps's pier in 1955-1956 (fide W. S. Bosworth).

**Diagnosis.** Female ov., **Holotype** (5.0 mm), 5 **Paratype** specimens, "Velero" Stn. 2312-53, collections of the Allan Hancock Foundation. Similar to *Eohaustorius washingtonianus*, with the following differences:

Mandible, palp segment 3, posterior margin with 9-10 (vs. 11) comb spines, and distal spines of outer margin more numerous (9-10 vs. 6-7). Maxilla 2, outer plate with 1 distal outer marginal plumose seta. Maxilliped, outer plate shorter, more slender; palp segment 3 less broadly expanded.

Gnathopod 1, segment 5 more deeply broadened distally. Gnathopod 2, basis, hind margin more heavily setose; segment 6 broadened distally.

Peraeopod 3, coxa, antero-distally angled, not rounded, lower margin nearly straight. Peraeopod 4, coxal plate subrectangular; segment 5, hind lobe short; segment 6 broadened medially.

Peraeopod 5, coxa shallower, hind lobe more richly setose behind; basis less broad; segment 6 relatively short broad, margins and apex with fewer spines. Peraeopod 6,

basis broadening distally; segment 4 slightly narrowing distally, facial spines few, weak; segment 5, facial spines few, distal excavation more pronounced. Peraeopod 7, basis with weaker proximal posterior cusp; segment 4 less broad distally; segment 5, anterior margin with 1 cluster of spines.

Pleon plate 3, hind corner more strongly produced, sharply acute, less exceeded by postero-dorsal process of pleon 3. Uropod 3, rami more slender, inner ramus with fewer inner marginal setae.

**Taxonomic commentary.** According to Bosworth (1973; personal communication), Barnard (1957, plate 1) incorrectly designated his subtidal material from southern California as *Eohaustorius washingtonianus*, mainly because of the pronounced cusp on the basis of peraeopod 7. However, Bosworth noted that the cusp is more strongly pronounced, and the ratio of segments 5 & 6 of peraeopod 5 is different in Thorsteinson's original northern species.

Other differences, noted in this study, include (in *E. barnardi*) the smaller size of maxilliped palp segment 3, the smaller size of the carpal lobe of peraeopod 4, the weaker facial armature of segments 4 & 5 of peraeopod 6, the less prominent hind lobe of segment 4 of peraeopod 7, and the more prominent and more strongly angled posterior process of pleon plate 3.

**Etymology.** We take pleasure in formally naming this species in honour of the late Dr J. L. (Jerry) Barnard who initially described and figured it, and who contributed inestimably to the advancement of knowledge of the systematics and biogeography of fossorial amphipod crustaceans.

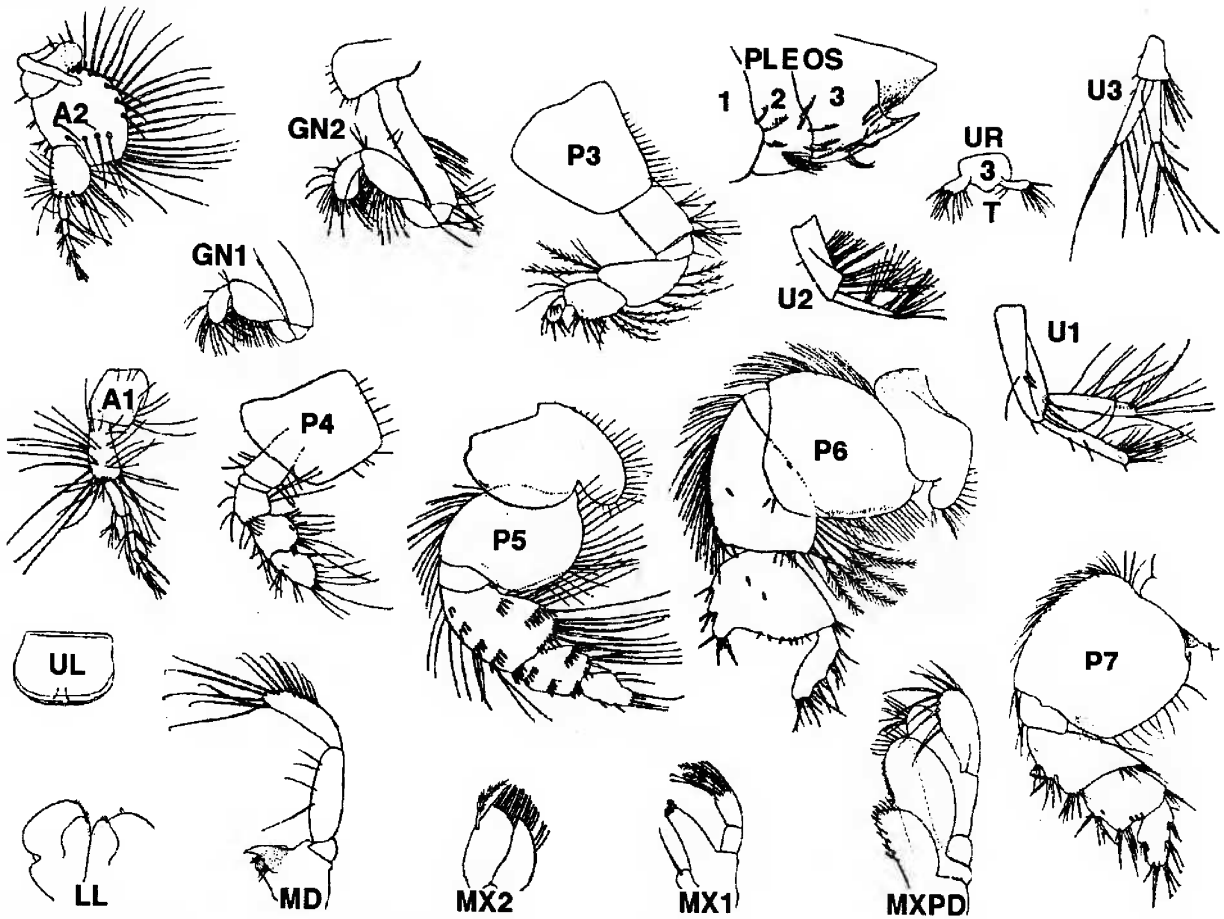


FIG. 13. *Eohaustorius barnardi*, new species. Female (5.0 mm). San Pedro shelf, ~15 m, California. (modified from Barnard, 1957).

*Eohaustorius cheliferus* (Bulycheva)  
(Fig. 14)

*Haustorius cheliferus* Bulycheva, 1952: 198, fig. 3.  
*Eohaustorius heliferus* Gurjanova 1962: 411, figs. 138A, B.  
*Eohaustorius cheliferus* Barnard & Karaman, 1991: 363.—  
Ishimarus, 1994: 64.

**Diagnosis:** Female ov (7.0 mm) Head broad, rostrum short, broadly acute. Eyes unpigmented. Antenna 2, peduncle 4, posterior lobe large, with 35+ marginal plumose setae, postero-distal lobe strongly produced, attaining end of segment 5; segment 5 broadest medio-distally; flagellar segment 1 with 3 postero-distal plumose setae. Mouthparts undescribed.

Gnathopod 1, basis, hind margin weakly setose; segment 5 shallow, not elongate; segment 6 broadest medio-distally, dactyl stout, unguis linear, longer than body. Gnathopod 2, basis, posterior margin distally setose; segment 5 slender, postero-distal spines each with medial cross-piece, distally toothed; segment 6 slender, short.

Peraeopod 3, coxa lunate, hind corner acute; basis broad, margins distally setose; segment 4 medium, distally broad, hind margin richly setose; segment 5 deep, hind margin heavily setose; segment 6 drop-shaped, margins lightly spinose. Peraeopod 4, segment 4, anterior oblique

row with stout spines, posterior margin with 3 long setae; segment 5 with strong anterior oblique spine row, posterior lobe large, long, postero-proximal margin with 4 clusters of spines and long setae, distal free margin bare; segment 6 small, overhung by lobe of 5, with single anterior marginal spine cluster, posterior marginal spines continuous with apical spines.

Peraeopod 5, basis broadening distally, postero-distal lobe faint, hind margin fully setose; segment 4 long, little broadened, facial spine rows strong; segment 5 subquadrate, facial spines strong; segment 6 medium, with single anterior and posterior marginal spine groups. Peraeopod 6, basis broad, hind margin strongly convex, setose proximally; segment 4 medium, broadest subapically, with 4-5 clusters of facial spines; segment 5 slightly broader distally, with single facial spine cluster, distal free margin with 7-8 spines, distal excavation medium deep; segment 6 short, curved forwards, hind margin with longish simple-tipped spines. Peraeopod 7, basis broad, hind margin nearly straight, distally weakly setose, lacking proximal cusp; segment 6 triangular, broadest distally, hind margin setose; segment 5 longer than broad, anterior margin with 2-3 spine clusters, distal free margin short; segment 6 medium broad, anterior margin with 1, posterior margin with 2, spine clusters

Pleon plate 3, hind corner acute, produced, apex acute slightly angled upwards; lower margin setose. Uropod 3,

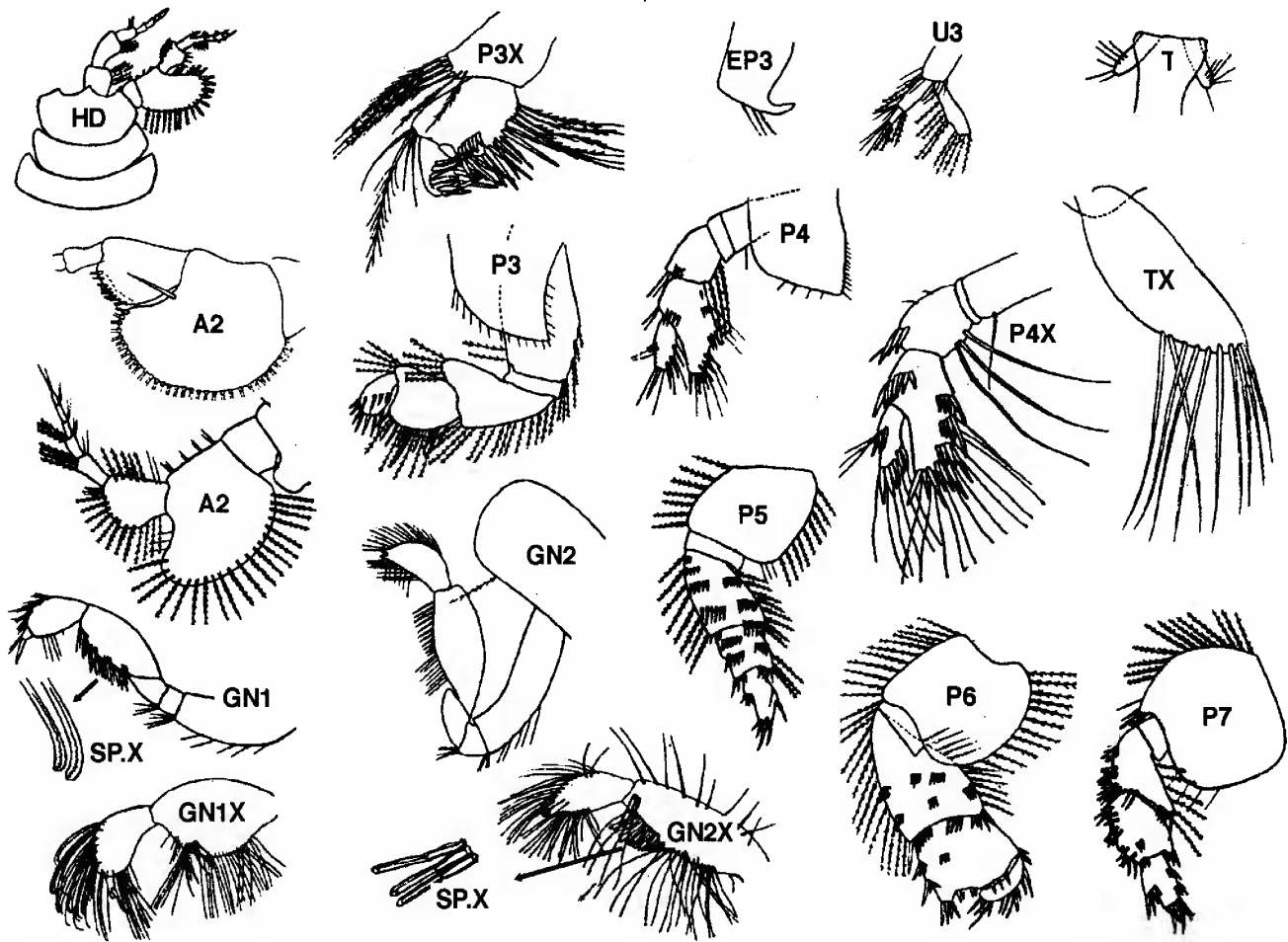


FIG. 14. *Eohaustorius cheliferus* (Bulycheva). Female ov (7.0 mm). Japan Sea to Sea of Okhotsk. (modified from Bulycheva, 1952)

rami medium; terminal segment of outer ramus medium; inner ramus, inner margin with 4-5 plumose setae. Telson lobes elongate, narrowly oval, with long dorso-distal setae.

**Distributional commentary.** Pacific coast of Iturup I, 30-40 m depth. Also recorded from the Sea of Japan (Peter the Great Bay) in depths of 0.75-13 m; also Sea of Okhotsk (Amur R. estuary and Aniv Bay) and Southern Kurile Strait, in depths of 6 - 40 m (Gurjanova, 1962).

**Taxonomic commentary.** The illustrations of Bulycheva (1952), repeated in Gurjanova (1962), are limited in detail but, in conjunction with her descriptive text, provide sufficient basis for reliable separation as a species distinct from all others of this study. As noted in the phenogram (p. 59) the species bears similarities to *E. longicarpus* of South Korean waters, and to *E. sencillus* of the North American Pacific coast, but is otherwise distinct from nearly everything else.

This species name may encompass a complex of closely related species. All materials listed by Gurjanova (1962) might therefore be re-examined for this possibility.

*Eohaustorius longicarpus*, new species  
(Fig. 15)

**Material examined.**

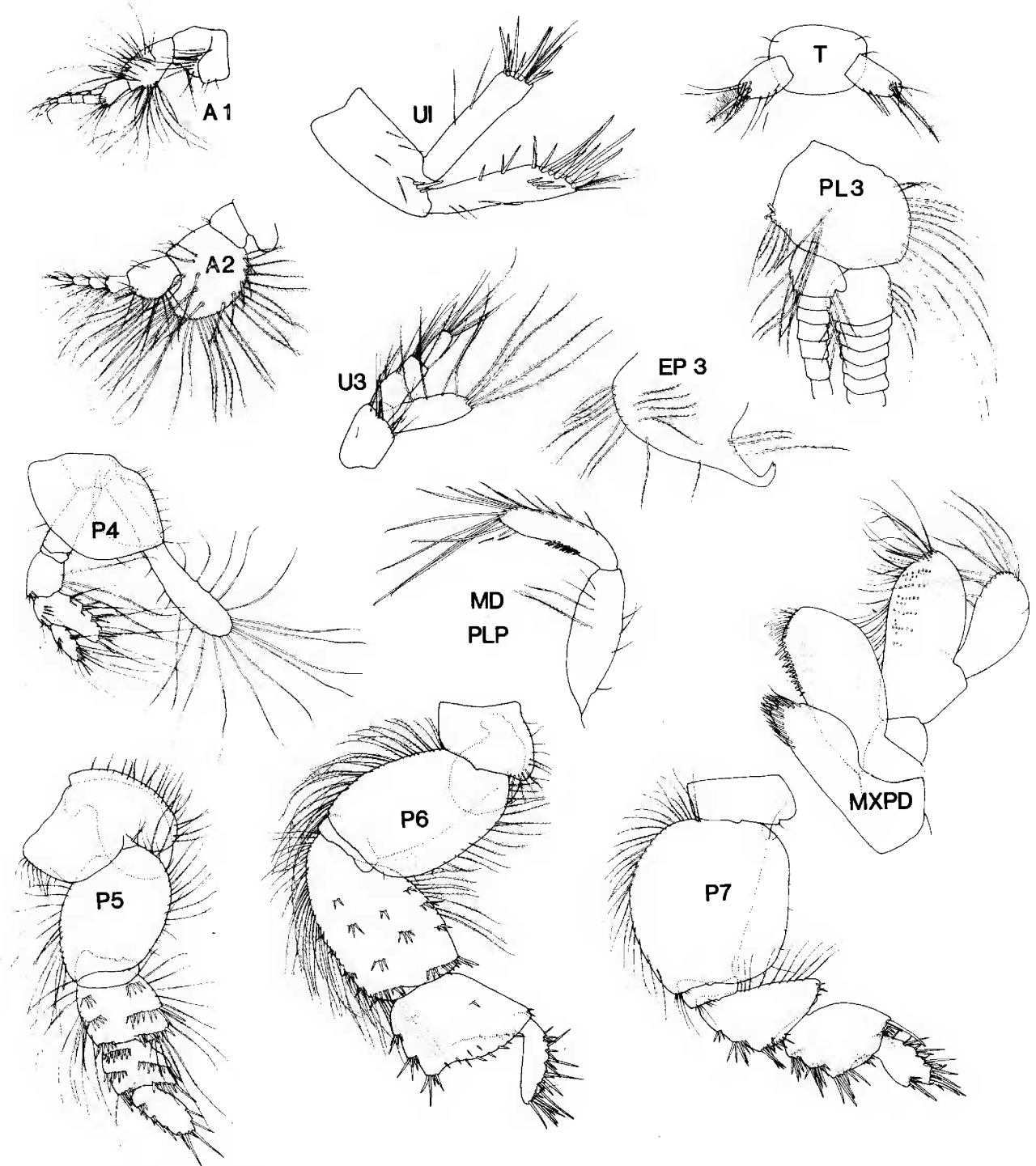
Pusan, South Korea, protected and beach at LW, Jae-Sang Hong coll., June, 1983. - Female ov (4.0 mm) **Holotype** (slide mount); male (4.7 mm), **Allotype** (slide mount); female ov. (3.5 mm), **Paratype**. CMN Cat. no. pending.

**Diagnosis.** Female ov (4.0 mm): Head, rostrum. Eyes. Antenna 1, peduncle 1, anterior margin proximally bare. Antenna 2, peduncle 4, hind lobe deep, margin with 20-25 plumose setae, postero-distal lobe large; segment 5 medially deepest; flagellar segment 1 with 1-2 postero-distal setae.

Mandible, palp segment 3 slender, posterior margin with 10 comb spines. Maxilliped, inner plate broad medially; outer plate large, broad but short; palp segment 2, inner lobe broad, large, extending almost to tip of slender segment 3.

Coxae 1 & 2 small, medium deep. Gnathopods 1 & 2 generally similar to those of *E. cheliferus*.

Peraeopod 3 ordinary. Peraeopod 4, coxa relatively



**FIG. 15. *Eohaustorius longicarpus*, new species. South Korea. Male (4.5 mm); female (4.0 mm).**

narrow, deep; basis slender, lacking distal setae; segment 4 with weak anterior oblique spine cluster, hind margin with 3 long plumose setae; segment 5 with anterior oblique row of slender spines, hind lobe elongate, proximal margin with 3 spine clusters, distal free margin bare; segment 6 slender, nearly exceeded by hind lobe of segment 5, anterior margin with 1, posterior margin with 2-3, groups of slender spines and setae.

Peraeopod 5, hind lobe of coxa narrow, deep, hind margin strongly setose; basis relatively slender, subovate,

lacking distinct postero-distal lobe; segment 4 short, uniformly broad, facial spine rows strong; segment 5 broader than long, facial spines strong; segment 6 broad, anterior margin with 3-4 singly inserted or groups of spines, hind margin distally with 2 slender spines. Peraeopod 6, basis little expanded distally broadest, with weak distal lobe, hind margin distally bare of setae; segment large, long, broad throughout, with 5-6 clusters of facial spines; segment 5 short, very broad distally, with 1 or 2 facial spines, and 5-7 distal margin spines, distal excavation very shallow; seg-

ment 6 straight, hind margin with 6-7 spines, long spines simple. Peraeopod 7, basis medium broad, hind margin nearly straight, nearly bare, lacking proximal cusp; segment 4 triangular, broadest distally, hind margin setose; segment 5 subquadrate, anterior margin with 2 spine groups, distal free margin with 1-2 small spine groups; segment 6 medium, broadest medially, anterior margin with 1, posterior margin with 3, clusters of slender spines.

Pleopods, peduncle large, broad; outer ramus with 15? segments, inner with 10 segments? Pleon plate 3, hind corner strongly produced, sharply upturned near apex, base of inner margin with 3 long setae. Uropod 1, rami subequal; peduncle, outer margin nearly bare, with 2-3 weak distal spines; inner ramus, posterior margin with 2 setae; outer ramus with a few posterior marginal spines. Uropod 3, rami relative short, thick, terminal segment long; inner ramus, inner margin with 4 long setae. Telson lobes short, thick, with 5-6 dorso-distal and a few inner marginal setae. Coxal gills short, saclike

**Etymology.** From *longi* - + *-karpos* (wrist), alluding to the elongate posterior lobe of the carpus of peraeopod 4.

**Distribution.** Known only subtidally from sand beaches in South Korea.

**Taxonomic and biogeographical commentary.** The species exhibits mainly pleisiomorphic character states, and clusters generally with the primitive *E. eous* complex (F.g. 16, p. 59). It is not closely related to any other species (well below 75% similarity levels) and the material is regrettably insufficient for biographic commentary.

## Discussion and Conclusions

In this study, the genus *Eohaustorius* was found to encompass 13 described species that are endemic to intertidal and shallow subtidal waters of the North Pacific marine region. Their sediment-burrowing and filter-feeding life styles are accompanied by limb adaptations that are grossly similar to, but much more highly specialized than, those of members of the North-Pacific endemic talitroidean family Dogielinotidae from which they are now phylogenetically separated (Bousfield & Tzvetkova, 1982; Barnard & Karaman, 1991). However, members of the Dogielinotidae are more advanced phylogenetically in having strongly sexually dimorphic gnathopods, and utilizing pre-plexing reproductive behaviour (Bousfield & Shih, 1994).

As noted previously (e.g. Barnard, 1957; Bousfield 1965), *Eohaustorius* is grossly similar in body form and limb structure to the 7 other genera of family Haustoriidae most of whose member species are endemic to the North American Atlantic region (Bousfield, 1970). However, the species of *Eohaustorius* are distinguished not only by their generally smaller size, but by their less highly specialized mouthparts, smaller coxae of gnathopods 1 & 2, unlike form of peraeopods 3 & 4, generally shorter, broader, and less spinose distal

segments of peraeopods 5-7, lack of a distal ventral lappet on urosome 1, more setose rami of uropod 3, and the widely separated (basally unfused) lobes of the telson, among other differences.

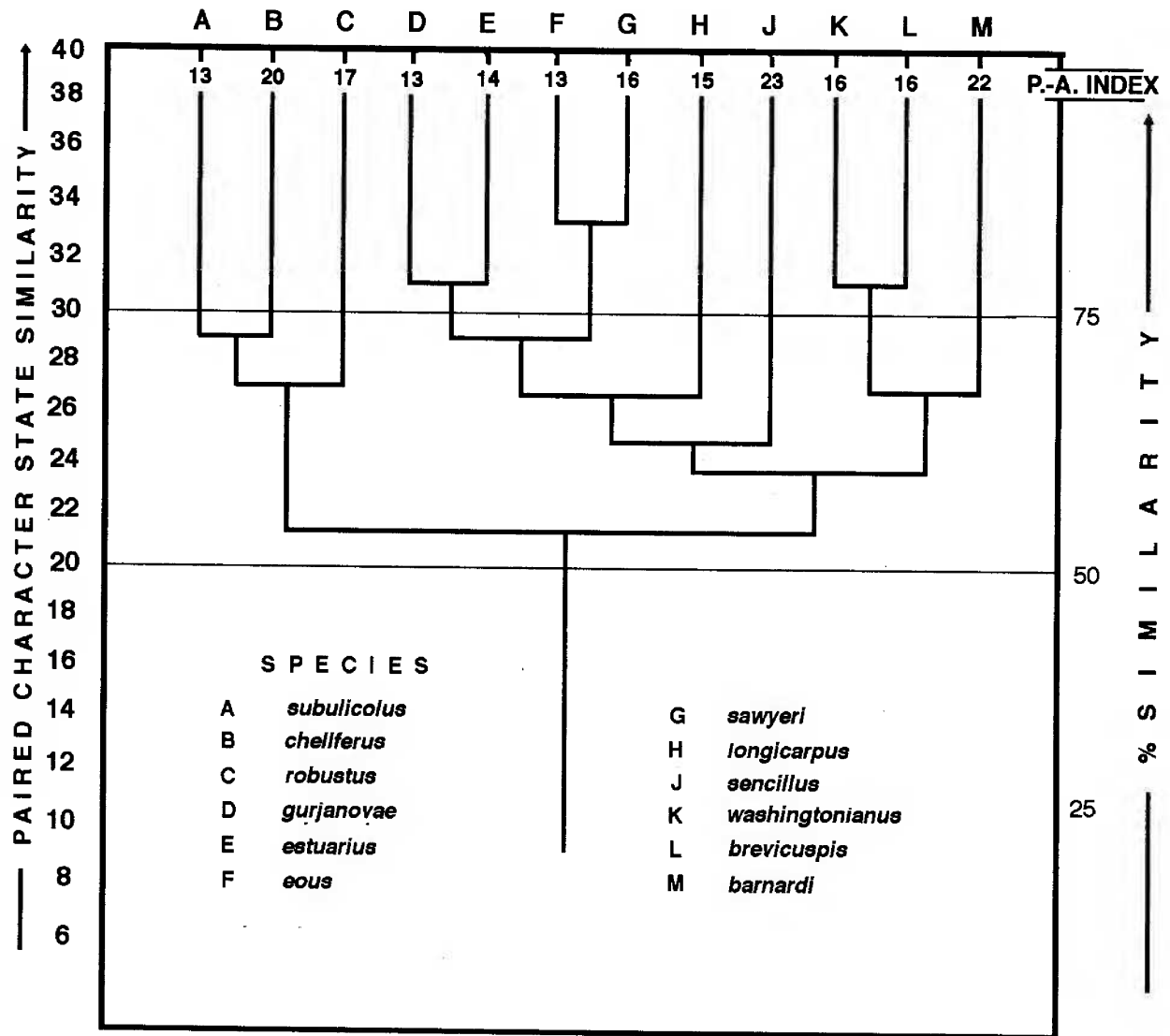
Concerning a common ancestry for these 8 genera, *Eohaustorius* appears least different from the genus *Pseudo-haustorius* Bousfield, 1965. Similar character states include those of: (1) antennae 1 & 2 (flagella short, few segmented); (2) maxilla 1 (weakly setose inner plate, lack of baler lobe); (3) maxilla 2 (plates relatively unmodified for filter feeding); (4) maxilliped palp (segment 3 claviform); (5) peraeopod 6 (segment 6 spatulate [vs. linear]); (6) pleon segment 3 (strongly produced dorso-distally, lateral plate acutely produced); (7) urosome 1 (peduncle and rami setose, weakly spinose); (8) urosome 2 (nearly occluded dorsally by urosome segments 1 & 3); (9) uropod 3 (terminal segment of outer ramus short) and (10) telson (lobes setose [vs. spinose]). Some of these character states (e.g., 6, 10), as well as the subrectangular form of segment 5 of peraeopod 6, are typical also of the genus *Acanthohaustorius*. Whether these similarities signify relatively close phyletic relationships or accrue mainly to similarities in lifestyle and habitat of component species is moot. If phyletic, morphological similarities would link two genera that appear to have little readily discernible biogeographical relationship (see p. 59). An alternative possibility, that the genus *Eohaustorius* evolved independently from a pontoporeiid ancestral group, and that the family Haustoriidae is therefore polyphyletic, receives little support from this analysis.

Within the genus *Eohaustorius*, numerical analysis of 20 selected morphological characters and pertinent character states of 12 of the 13 described species is summarized in a phenogram of species similarities (Table I; Fig. 12). The present modification of the UPGMA cluster analysis system of Sneath & Sokal (1973) has been used in similar studies of other North Pacific amphipod groups (e.g., Conlan, 1983; Jarrett & Bousfield, 1994). Here the analysis is slightly compromised by limited morphological information available concerning mouthparts of some western North Pacific species. Despite the unavoidable emphasis on character states that may reflect burrowing behaviour rather than phyletic relationships, the overall results are considered significant.

In the phenogram (Fig. 16) three main groups "cluster out" at better than 60% similarity levels. In the centre is a relatively primitive *eous* group of six species, from both Asiatic and North American coastal regions, having P.-A. indices mainly of 13-16, but 23 for the somewhat isolated *E. sen-cillus*. The core group is flanked on the left by the somewhat aberrant Asiatic *cheliferus* group, with P.-A. indices of 13-20, and on the right by the North American *washingtonianus* group, with P. A. Indices of 16-22. The *cheliferus* group is characterized by strongly produced and/or distally hooklike hind corner of pleon plate 3 relatively strongly spinose hind margin of segment 6 of peraeopod 5, slender telson lobes, low numbers of comb spines on mandibular palp segment 3, and well-developed hind lobe of segment 5, peraeopod 4. Members of the *washingtonianus* group have a proximal



FIG. 16. PHENOGRAM OF NORTH PACIFIC SPECIES OF *EOHAUSTORIUS*\*



\* except *E. tandeensis* Dang, 1968

cus on the posterior margin of the basis of pereopod 7, one spine cluster on the postero-distal margin of segment 5 of pereopod 4, and a relatively large maxilliped palp segment 3. The core *eous* group shows mainly plesiomorphic character states, including a relatively elongate, facially and marginally spinose, segment 4 of pereopod 6 that typifies most Atlantic genera of haustoriinids. *E. sencillus* is uniquely advanced in its very short antennal flagella, enlarged dactyl of gnathopod 1, and short maxilliped palp segment 3. All in all, few species pairings exhibit greater than 75% similarity and none is closely related, suggesting long periods of isolation and limited gene flow between populations. The relatively primitive nature of intertidal vs. subtidal species of *Eohaustorius* is consistent with similar trends in other regional fossorial amphipods (e.g. Jarrett & Bousfield, 1994a).

**Biogeographical Considerations**

The subregional occurrence of species of *Eohaustorius* is provided in Table II. Of the twelve species considered here, five are endemic to Asiatic North Pacific shores, and six to the North American coast. Only one species, *E. eous*, occurs in both continental waters, and only in the Bering Sea region.

In the Asiatic region, *E. robustus* and *E. cheliferus* are confined mainly to the Sea of Okhotsk and Kamchatka regions whereas *E. gurjanovae*, *E. longicarpus* and *E. subulicolus* have been recorded exclusively or mainly from southern Sakhalin Island and the Sea of Japan. In the more southerly region, these haustoriid species overlap distributionally, in similar sedimentary habitats, with members of the talitroidean fossorial family Dogielinotidae. The dogiel-

**TABLE I. CHARACTERS AND CHARACTER STATES OF SPECIES OF *EOHAUSTORIUS***

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Antenna 2, peduncle 4, number of posterior marginal setae	<20	25	>30
2. Antenna 2, flagellar segment 1, number postero-distal long setae	1	2	3+
3. Mandibular palp segment 3, number of posterior marginal comb spines	10+	7	5
4. Maxilliped palp, segment 3, size	Large		Small
5. Peraeopod 3, coxal shape	Squarish		Semilunate
6. Peraeopod 4, hind lobe of segment 5	Short W>L		Long L>>W
7. Peraeopod 4, segment 5, hind lobe, distal marginal spines	Absent		Present
8. Peraeopod 5, length of segment 4	Long		Short
9. Peraeopod 5, shape of segment 5	Narrow		Wide
10. Peraeopod 5, segment 6, number of posterior marginal spines	2 - 3		1
11. Peraeopod 6, length of segment 4	Long L>>W		Short W=L
12. Peraeopod 6, segment 5, number of anterior marginal spine clusters	2		1
13. Peraeopod 6, segment 4, hind marginal spines	1+		0
14. Peraeopod 7, basis, proximal hind marginal cusp	lacking		present
15. Peraeopod 7, segment 5, number of anterior marginal spine clusters	2-3		1
16. Peraeopod 7 segment 6, number of posterior marginal spine clusters	3-4	2	1
17. Pleon plate 3, type of hind process	short	medium straight	long, hooked
18. Uropod 1, inner ramus, number of posterior marginal setae	5+	2	0
19. Uropod 3, size of terminal segment of outer ramus	Long		short
20. Telson lobes, form.	elongate		short

TABLE II. DISTRIBUTION OF NORTH PACIFIC SPECIES OF *EOHAUSTORIUS*

SPECIES	BIOGEOGRAPHICAL ZONES								
	1	2	3	4	5	6	7	8	9
<i>E. subulicolus</i> <sup>^</sup>	X								
<i>E. longicarpus</i> <sup>^</sup>	X								
<i>E. gurjanovae</i> <sup>^</sup>	X	x							
<i>E. cheliferus</i> <sup>^</sup>	x	X							
<i>E. robustus</i> <sup>^</sup>		X							
<i>E. eous</i> <sup>^</sup>		X	X						
<i>E. estuarius</i> *				?	X	X	X	?	
<i>E. washingtonianus</i> *				X	X	X	X	x	
<i>E. brevicuspis</i> *						x	X	X	
<i>E. sawyeri</i> *						x	X	X	x
<i>E. sencillus</i> <sup>^</sup>							X	X	x
<i>E. barnardi</i> <sup>^</sup>								x	X

ZONES: 1. Japan Sea and southward 2. Sea of Okhotsk region 3. Bering Sea -W. Alaska  
 4. Southeastern Alaska 5. Northern British Columbia 6. Southern British Columbia  
 7. Washington-Oregon 8. North & Central California 9. Southern & Baja California

Ecology: \* Intertidal; ^ Subtidal

inotid species, of similar or slightly larger size, tend to occur mainly intertidally, during summer months at least, along sandy beaches and in estuaries, often in very high densities (Kamihira, 1981; Bousfield & Tzvetkova, 1982). The northernmost beaches are subject to freezing and ice scour, especially during the winter and early spring, during which time the dogielinotids shift from the littoral to the infralittoral zone. The regional haustoriid species occur subtidally, at least during summer months, and probably year-round. Perhaps intense competition with the filter-feeding and "sand-licking" dogielinotids in summer, and rigorous physical conditions in winter, are factors that have apparently prevented evolution of Asiatic regional intertidal haustoriid species.

Along North American Pacific sandy shores however, the situation is strongly contrasting. Of the six species recorded from southeastern Alaska to southern California,

the four northernmost species, *E. estuarius*, *E. washingtonianus*, *E. brevicuspis* and *E. sawyeri* occur essentially intertidally and shallow sublittorally. As noted on page 59, and in figure 16, these northern species show mostly plesiomorphic character states and probably evolved early during the penetration of the genus into the North Pacific region. The two southernmost species, *E. sencillus* and *E. barnardi*, are strictly subtidal and their character states are significantly more advanced. However, the northern intertidal species and one southern subtidal species (*E. sencillus*) all co-occur in biogeographical zone 6 (Washington-Oregon), the very region in which the single North American dogielinotid species, *Proboscinothus loquax* (Barnard, 1967) occurs intertidally in great abundance (Hughes, 1982). This species, and *Eohaustorius brevicuspis*, co-occur intertidally on open surf sand beaches and are

presumed to be heavily preyed upon by shore birds, especially during late summer. However, despite these negative factors of competition and predation, intertidal haustoriids are able to occur commonly throughout zone 6, and indeed zones 4-9, almost certainly because of year-round near uniformity of coastal marine conditions; water temperature seldom fall below 5°C, and winter ice scour is non-existent (Thomson, 1981). These near-uniform physical conditions probably account for the relatively wide geographical range of the North American species, each of which occurs in 3-5 biogeographical zones vs. the 1-2 zones of the Asiatic species.

With respect to its overall biogeographical affinities, *Eohaustorius* is essentially a cold temperate genus and, in this respect, closer to the presumed para-ancestral pontoporeiid and perhaps distantly ancestral gammaroidean groups that are restricted to holarctic regions (Bousfield, 1970; Bousfield & Shih, 1994). In the North Pacific, members of the genus *Eohaustorius* occur well north of 60° north latitude, and into the Bering Sea region, but apparently not into arctic waters where the Pontoporeiidae dominate (Bousfield, 1987). In the western North Atlantic region, however, the 7 haustoriid genera are essentially temperate, and warm-temperate in thermal requirements. Species of the most eurytopic genus, *Haustorius*, range along North American shores north only to latitude 47° (southern Gulf of St. Lawrence) where they appear to be limited intertidally by the severity and duration of winter conditions (Bousfield, 1965). In western Europe, however, where winter conditions are relatively mild and reminiscent of those of the western north Pacific, the species *H. arenarius* attains 60° north latitude (southern Norway) (Lincoln, 1979).

In conclusion, we have noted on p. 59 that *Eohaustorius* is grossly similar morphologically to the North Atlantic complex of haustoriid genera, but is here found biogeographically unrelated to them. In absence of firm evidence to the contrary, the genus *Eohaustorius* is here surmised to have been isolated in the North Pacific for a considerable period of time. An hypothetical subtidal common ancestor may have connected it directly to the relatively primitive North Atlantic genus, *Pseudohaustorius*, possibly during the early Miocene epoch. At that time, the Panama isthmus had not yet formed and suitably cool marine connections existed between Atlantic and Pacific coastal marine regions (Adams, 1981). Although such an explanation is not entirely satisfactory, it does accord reasonably with rationale proposed for similar Pacific-Atlantic disjunct distributions in other amphipod groups. Thus, in some members of the fossorial phoxocephalid genus *Eobrolgus* (Jarrett and Bousfield, 1994b) and in two species of the non-substrate modifying parapleustin genus *Incisocalliope* (Bousfield and Hendrycks, 1995), the distributional hiatus and its explanation may be similar, but the evidence for it appears to be more compelling.

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